

The giant pill-millipedes of Madagascar: revision of the genus *Zoosphaerium* (Myriapoda, Diplopoda, Sphaerotheriida)

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ABSTRACT

All available type material of the genus *Zoosphaerium* Pocock, 1895, which includes 27 of 37 described species, is revised. Seven new synonyms are established: *Z. stridulator* (de Saussure & Zehntner, 1902) junior synonym of *Z. blandum* (de Saussure & Zehntner, 1902); *Z. digitale* (de Saussure & Zehntner, 1897) and *Z. pygidiale* (de Saussure & Zehntner, 1897) junior synonyms of *Z. neptunus* (Butler, 1872); *Z. imbecillum* (de Saussure & Zehntner, 1897) and *Z. globulus* (de Saussure & Zehntner, 1902) junior synonyms of *Z. voeltzkowianum* (de Saussure & Zehntner, 1897); *Z. amittum* Chamberlin, 1921 and *Heligmasoma errans* Chamberlin, 1921 junior synonyms of *Z. coquerelianum* (de Saussure & Zehntner, 1897). The genus *Heligmasoma* Chamberlin, 1921 and the subgenus *Globotherium* Brolemann, 1922 are both junior synonyms of *Zoosphaerium* Pocock, 1895. For nine species (*Zoosphaerium actaeon*, *Z. reflexum*, *Z. elegans*, *Z. crassum*, *Z. stigmaticum*, *Z. glabrum*, *Z. latum*, *Z. lamprinum* and *Z. testaceum*), no types could be detected in collections, so these names are to be *nomina dubia*. Eighteen Malagasy species are redescribed, with drawings of all structures of taxonomic importance and SEM micrographs presented here for the first time. The type material is compared with giant pill-millipede material collected during general species inventories on Madagascar conducted during the 1990s and in 2003 by different institutions, altogether comprising more than 70 morphospecies, from which eight species could be assigned to a species name. A key to Malagasy Sphaerotheriida is presented. The status of the genus *Zoosphaerium* is discussed. Some of the species can already be placed in preliminarily outlined species-groups.

KEY WORDS

Myriapoda,
Diplopoda,
Sphaerotheriida,
Zoosphaerium,
Globotherium,
Heligmasoma,
Madagascar,
revision.

RÉSUMÉ

Les mille-pattes géants de Madagascar : révision du genre Zoosphaerium (Myriapoda, Diplopoda, Sphaerotheriida).

Tout le matériel disponible du genre *Zoosphaerium* Pocock, 1895, qui contient 27 des 37 espèces décrites, a été examiné. Sept nouvelles synonymies sont établies : *Z. stridulator* (de Saussure & Zehntner, 1902) synonyme plus récent de *Z. blandum* (de Saussure & Zehntner, 1902) ; *Z. digitale* (de Saussure & Zehntner, 1897) et *Z. pygidiale* (de Saussure & Zehntner, 1897) synonymes plus récents de *Z. neptunus* (Butler, 1872) ; *Z. imbecillum* (de Saussure & Zehntner, 1897) et *Z. globulus* (de Saussure & Zehntner, 1902) synonymes plus récents de *Z. voeltzkowianum* (de Saussure & Zehntner, 1897) ; *Z. amittum* Chamberlin, 1921 et *Heligmasoma errans* Chamberlin, 1921 synonymes plus récents de *Z. coquerelianum* (de Saussure & Zehntner, 1897). Le genre *Heligmasoma* Chamberlin, 1921 et le sous-genre *Globotherium* Brolemann, 1922 sont tous les deux des synonymes plus récents de *Zoosphaerium* Pocock, 1895. Les types de neuf espèces (*Zoosphaerium actaeon*, *Z. reflexum*, *Z. elegans*, *Z. crassum*, *Z. stigmaticum*, *Z. glabrum*, *Z. latum*, *Z. lamprinum* et *Z. testaceum*) n'ont pu être localisés dans les collections. Nous proposons donc de traiter ces noms comme *nomina dubia*. Dix-huit espèces malgaches sont redécrites, avec des dessins de toutes les structures d'importance taxonomique et micrographies MEB présentés ici pour la première fois. Le matériel type est comparé à celui des mille-pattes géants ramassé pendant les inventaires généraux conduits pendant les années 1990 et en 2003 par diverses institutions, comprenant en tout plus de 70 morphospecies, parmi lesquelles huit peuvent être assignées à un nom d'espèce. Une clé de détermination des *Sphaerotheriida* malgaches est présentée et le statut du genre *Zoosphaerium* est discuté. Une partie des espèces sont placées dans des groupes d'espèces préliminaires.

MOTS CLÉS

Myriapoda,
Diplopoda,
Sphaerotheriida,
Zoosphaerium,
Globotherium,
Heligmasoma,
Madagascar,
révision.

INTRODUCTION

Madagascar is famous for its diverse, highly endemic and critically endangered fauna and flora (Myers *et al.* 2000; Lowry *et al.* 2001). Giant pill-millipedes (order Sphaerotheriida Brandt, 1833) are one of the most conspicuous groups among invertebrates because of their gigantic size and species richness. This order, with more than 240 described species, is represented in Madagascar by members of the subfamily Arthrosphaerinae Jeekel, 1974, containing the Indian tribe Arthrosphaerini and the endemic Malagasy tribe Zoosphaeriini Jeekel, 1974, the latter with 40 species (Jeekel 1974, 1999; Enghoff 2003; Wesener & Sierwald 2005a, b). The Zoosphaeriini are somewhat special because some of the species are much larger than related taxa in other distribution areas. The largest known Malagasy sphaerotheriid is

a female of an undescribed species in the collections of the MNHN with a body length of 95.5 mm and a width of 46.35 mm, reaching a size comparable to an orange when rolled up. In comparison, the largest South African species, *Sphaerotherium giganteum* Porat, 1872, reaches a body length up to 55 mm (Van den Spiegel *et al.* 2002, and pers. obs.). Furthermore, Zoosphaeriini have another feature, unique in the whole class Diplopoda: both females and males possess a stridulation organ (Figs 3C; 11B; 22D; 35A), the female “washboard”-type and the male “harp”-type (de Saussure & Zehntner 1902).

On Madagascar, giant pill-millipedes are, after the Spirostreptida and before the Spirobolida, the second millipede order in terms of species richness (Enghoff 2003). They are represented on Madagascar by three genera, the enigmatic Indian-Malagasy missing link *Sphaeromimus* de Saussure &

Zehntner, 1902 (see Wesener & Sierwald 2005b for a revision), the recently discovered, strongly adapted dwarf-genus *Microsphaerotherium* Wesener & Van den Spiegel, 2007 and the bulk of the species (37 of 41) in *Zoosphaerium* Pocock, 1895.

Despite such a conspicuous appearance, species richness and possibly even ecological importance (Ashwini & Sridhar 2002; Lawrence & Samways 2003), Malagasy giant pill-millipedes are poorly known, with the genus *Zoosphaerium* and almost all species in urgent need of revision (Jeekel 1974, 1999; Hoffman 1980). This made Jeekel (1974: 52) state that "The Madagascan fauna, for instance, should be re-investigated, most of it is incompletely known."

The first Malagasy giant pill-millipede was described by Olivier (1792), succeeded by Gervais (1847, one species) and White (1859, one species). More species were described by Butler (1872, 1873, 1878, eight species), some years later by Lenz (1880, one species) and Karsch (1881, one species), the latter two authors presenting for the first time more than a habitus drawing. The largest number of species (17) were described by de Saussure & Zehntner (1897, 1901, 1902), whereas in the 100 years before 2005 only six more species were added by Attems (1910, one species), Chamberlain (1921, two species), Brolemann (1922, two species) and Jeekel (1999, one species). The species descriptions are of different scientific value and not a single revision was attempted until 2005! Generally, almost no Malagasy giant pill-millipede is identifiable based on the literature alone. Further progress in sphaerotheriid systematics was also blocked by too few taxonomically useful characters being known at that time. These not very encouraging circumstances were the main motivation for conducting this study. In the last few years, many new characters have been detected or rediscovered (Van den Spiegel *et al.* 2002; Wesener & Sierwald 2005a, b), for example the endotergum (Fig. 4C-F), which is the underside of the tergites.

The unclear position and synonymies inside *Zoosphaerium* blocked all further work on this group. Recent field collecting, conducted by American institutions in 34 localities, revealed more than 70 morphospecies of *Zoosphaerium*, most of them endemic to a single area of Madagascar, sometimes even a single remaining forest (Wesener & Sierwald 2005a, b).

Because of the fast ongoing destruction of natural vegetation on Madagascar (Green & Sussman 1990; Myers *et al.* 2000; Lowry *et al.* 2001; de Gouvenain & Srilander 2003), description and identification of the species became urgent as never before. The aim of this study is to present redescrptions of all known Malagasy giant pill-millipede species, providing characters which will allow a secure determination to the species level for the first time.

MATERIAL AND METHODS

The types of the species were received on loan from different museums (BMNH, ZMB). The type material of Gervais and de Saussure & Zehntner, which was not available for loan, could be studied during a one-month internship in February 2005 at the MNHN. Undetermined material was lent from the MHNG, CAS and FMNH; additional undetermined material could be detected by the author in the bulk collection at the MNHN.

Pencil drawings were made using a camera lucida. Habitus drawings were made after photos of the specimens taken using a Ricoh Caplio RR30. SEM objects were dehydrated in an alcohol series, mounted on stubs and dried overnight. Ultrasonic cleaning of the endotergum was not attempted, being too damaging for old material. Many of the structures taken from type specimens are thus still covered with dirt. The stubs were coated with gold and observed using a Zeiss DSM 950. All measurements are in millimeters, if not indicated otherwise. For the use of zoological terms in Sphaerotheriida see Wesener & Sierwald (2005b). The only change occurred in the naming of sternites. The plates lateral to sphaerotheriid legs bearing the tracheal opening seem more likely to be pleurites than sternites, whereas the real sternites are completely reduced (Snodgrass 1958). However, those structures are named "stigma-carrying plates" in this paper to avoid confusing the reader. The plates named pleurites in previous papers seem to represent laterotergites (see also Snodgrass 1958).

ABBREVIATIONS

BLF Brian L. Fisher, internal collection codes for samples at the CAS;

BMNH	The Natural History Museum, London;
CAS	California Academy of Sciences, San Francisco;
FMMC	Field Museum Millipede Collection. Internal collection codes of the FMNH;
FMNH	Field Museum of Natural History, Chicago;
juv., juvs	juvenile(s);
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts;
MGF	Internal collection codes for Madagascar samples at the CAS;
MHNG	Muséum d'Histoire naturelle, Geneva;
MNHN	Muséum national d'Histoire naturelle, Paris;
SEM	scanning electron microscopy;
ZMB	Museum für Naturkunde der Humboldt-Universität, Berlin;

Subfamily ARTHROSPHAERINAE Jeekel, 1974

DIAGNOSIS. — Females with stridulatory organ (called washboard) consisting of sclerotized ribs on subanal plate and a sclerotized spot on posterior side of legs.

REMARK

Subfamily endemic to India, Sri Lanka and Madagascar.

Tribe ZOOSPHAERIINI Jeekel, 1974

DIAGNOSIS. — Tribe of Arthrosphaerinae with stridulatory organ (called harp) consisting of sclerotized ribs on first joint of male anterior telopods and one sclerotized spot on posterior side of legs.

INCLUDED GENERA. — *Sphaeromimus* de Saussure & Zehntner, 1902, *Microsphaerotherium* Wesener & Van den Spiegel, 2007 and *Zoosphaerium* Pocock, 1895.

REMARK

Tribe endemic to Madagascar. Such a stridulation organ was also recently discovered by the author in some Indian Arthrosphaerinae. At this point it is not clear if the tribe Zoosphaeriini in the current sense is monophyletic.

SYSTEMATICS

Family SPHAEROTHERIIDAE Jeekel, 1974

DIAGNOSIS. — Outer and inner parts of the vulva always surrounding the base of the operculum (Jeekel 1974).

REMARK

It is unclear if the family in the current sense is monophyletic.

KEY TO MALAGASY GIANT PILL-MILLIPEDE GENERA

1. Anterior telopods with four joints above syncoxite. Harp on first joint with three or more stridulation ribs. Vulva with large and well-rounded operculum, protruding up to half of prefemur length. Sixth joint of antenna broad, with more than 40 sensory cones. Legs with single, well-developed coxal lobe. Underside of anal shield with one black locking carina on each side. Neither groove nor sclerotized teeth on antennal joints *Sphaeromimus* (3 species, see Wesener & Sierwald 2005b for a revision)
- Anterior telopods with three joints above syncoxite. Harp on first joint with one or two stridulation ribs. Vulva with operculum, medially notched (subreniform) or operculum well-rounded, but not surpassing coxa (Figs 1D; 15C). Legs without coxal lobe. Underside of anal shield with zero, one or two black locking carinae on each side. Sixth joint of antenna cylindrical, with four or up to 45 sensory cones. At least first joint of antenna with sclerotized teeth 2
2. Underside of the anal shield on each side with two black locking carinae completely fused into a single large carina. First joint of antenna with small sclerotized teeth. Anal shield covered with large grooves and special-shaped, stout setae. Specimens smaller than 20 mm *Microsphaerotherium* Wesener & Van den Spiegel, 2007
- Underside of the anal shield with zero or two black locking carinae on each side. First joint of antenna with scale-like, sclerotized teeth. Anal shield not covered with large grooves and special-shaped, stout setae *Zoosphaerium* (37 species)

Genus *Zoosphaerium* Pocock, 1895

Zoosphaerium Pocock, 1895: 410. — Chamberlin 1921: 59. — Jeekel 1970: 29, 1974: 45, 1999: 5. — Enghoff 2003: 618.

Globotherium Brolemann, 1922: 230. Type species: *Sphaerotherium digitale* de Saussure & Zehntner, 1897, tentatively synonymized by Jeekel 1999: 9. — Enghoff 2003: 619, tables 8-19 (all *Globotherium* species assigned to *Zoosphaerium*).

Helignasoma Chamberlin, 1921: 58, n. syn. Type species: *Helignasoma errans* Chamberlin, 1921, synonym of *Zoosphaerium coquerelianum* (de Saussure & Zehntner, 1897).

TYPE SPECIES. — *Sphaerotherium neptunus* Butler, 1872, by subsequent designation by Pocock 1895.

DIAGNOSIS. — Head with numerous hairs and hair-pits, particularly around labrum and laterally of eyes. Body

length of adults 20-95.5 mm. Legs without coxal lobe. Stigma-carrying plates 3-21 with single, spine-like process almost reaching up to the stigma opening of more anterior plate. Anterior telopods with fused syncoxite followed by three joints. Harp on first joint of anterior telopods with 1 or 2 stridulation ribs. Both male and female stridulation ribs never as regularly developed as in *Sphaeromimus*. First antennal joint with sclerotized teeth. Apical antennal joint cylindrical, with disc carrying a variable number (4 to 60) of sensory cones. Bristles of endotergum scaly. Two or 0 (never only 1) black locking carinae inside of anal shield. Cyphopod sclerites consisting of 2 triangular apical sclerites and a much larger third sclerite formed like a tuning-fork, all visible as dark structures near suture between inner and exterior plate.

REMARK

It is unclear if the genus *Zoosphaerium* in the current sense is monophyletic.

KEY TO THE SPECIES-GROUPS OF *ZOOSPHAERIUM*

1. Inner margin of anal shield with two well-visible black locking carinae, both carinae of same length and located closely to anal shield margin (Figs 1C-E; 7B). Both pairs of telopods elongated (Fig. 2). Anterior telopods with only 1 stridulation rib, third joint without cavity (Fig. 2A-E). Third joint of posterior telopods without any spines or sclerotized spots (Fig. 2F-I) *Zoosphaerium neptunus* species-group
— Third joint of posterior telopod at least with small sclerotized spots (Figs 10K; 20K) ... 2
2. Third joint of posterior telopods on its backside with more than 15 large, black, sclerotized teeth, hollowed-out margin towards second joint with 2 large membranous lobes (Figs 10K; 14L) *Zoosphaerium libidinosum* species-group
— Third joint of posterior telopods without large teeth, or if black teeth present, then 2 large lobes not visible 3
3. Third joint of posterior telopods remarkably thick, 1-2.5 times longer than wide, with single well-rounded tip. Hollowed-out margin towards second joint present only in apical part of third joint (Figs 20J, K; 30K, L) 4
— Third joint of posterior telopods slim or of normal width. Tip often curved or pointed. Hollowed-out margin towards second joint often present on entire inner surface of third joint (Figs 34J, K; 38G-J) 5
4. Locking carinae of anal shield located closely to anal shield margin. Posterior (2nd) carina 2.5-4 times longer than anterior carina. Apical margin of operculum extended into 2 well-rounded lobes (Fig. 21A, B). Third joint of posterior telopods tapering apically, sclerotized spots present only on its posterior side, joint 2-2.5 times longer than wide (Figs 20J, K; 23K, L) *Zoosphaerium coquerelianum* species-group
— Locking carinae of anal shield located closely to last pair of laterotergites, far from anal shield margin. Second carina up to twice longer than first. Third joint of posterior telopods often greatly enlarged, less than twice longer than wide. Sclerotized spots on third joint of posterior telopods present often not only on posterior, but also on anterior side (Fig. 30J, K). First pair of stigma-carrying plates often greatly enlarged (Fig. 30B, C).

Apical margin of operculum extended into 2 lobes with sharp, pointed tips (Fig. 30F).
 Female washboard on each side with single, strongly developed stridulation rib
 *Zoosphaerium platylabum* species-group

5. Third joint of posterior telopods slim and surpassing second joint with 1/3 of its length.
 Width of second joint process as large or greater than width of third joint (Fig. 34J, K).
 Process of posterior telopods second joint always visible in anterior view (Fig. 34G)
 *Zoosphaerium piligerum* species-group
 — Characters not as above species non assigned to a species-group

Zoosphaerium neptunus species-group

SPECIES INCLUDED. — *Zoosphaerium neptunus* (Butler, 1872); *Z. campanulatum* (de Saussure & Zehntner, 1897).

DISTRIBUTION. — Rainforest and montane rainforests on Madagascar, particularly in the northern half of the island (Fig. 6).

DIAGNOSIS. — These Malagasy giant pill-millipede species share almost identical anterior and posterior telopods (Figs 2A-I; 7E-H) and furthermore in males a more or less bell-shaped anal shield (Figs 1A; 7D). All species included

possess 2 locking carinae of identical size on the ventral side of the anal shield (Figs 1C, D; 7B). The third joint of the posterior telopods is elongated, straight and without any trace of sclerotized teeth, lobes or spines, which is a unique feature in sphaerotheriids (Figs 2F, G; 7G, H). The process of second joint is long, slender, curved towards the third joint and without spines (Figs 2F, G; 7G, H). Similarities can also be found in the anterior telopods, which are elongated in appearance, all joints being longer than wide (Figs 2A-E; 7E, F). A phylogenetic analysis will be necessary to confirm if the *neptunus*-group represents a monophyletic group to be kept separately from the other Malagasy sphaerotheriids. The missing sex of *Z. campanulatum* is especially necessary to solve this problem.

KEY TO THE *ZOOSPHERIUM NEPTUNUS* SPECIES-GROUP

1. Anal shield in males weakly bell-shaped. Third joint of posterior telopods slim with pointed tip (Fig. 2G) *Z. neptunus*
 — Anal shield in males strongly bell-shaped. Third joint of posterior telopods broad with stout tip (Fig. 7G) *Z. campanulatum*

Zoosphaerium neptunus (Butler, 1872) (Figs 1-5)

Sphaerotherium neptunus Butler, 1872: 358, pl. 18, fig. 6. — de Saussure & Zehntner, 1902: 67.

Zoosphaerium neptunus – Pocock 1895: 410. — Jeekel 1999: 10 (lists species name). — Enghoff 2003: 620 (lists species name).

Sphaerotherium digitale de Saussure & Zehntner, 1897: pl. 5, fig. 16, n. syn.

Sphaerotherium pygidiale de Saussure & Zehntner, 1897: pl. 5, figs 8-8d, n. syn.

Sphaerotherium lamprinum – de Saussure & Zehntner 1897: pl. 5, figs 17-17b (redescription). Not *S. lamprinum* Butler, 1878.

Sphaerotherium latum – de Saussure & Zehntner 1897: pl. 5, fig. 14 (redescription). Not *S. latum* Butler, 1872.

Sphaerotherium hippocastanum – de Saussure & Zehntner 1897: pl. 5, fig. 15 (redescription). Not *S. hippocastanum* Gervais, 1847.

Sphaerotherium (Globotherium) digitale – Brolemann, 1922: 232, figs 6-8.

TYPE MATERIAL. — *Zoosphaerium neptunus*: Madagascar, ♀ holotype in parts (BMNH BM.1858.85).

Z. digitale: Madagascar, Antananarivo, 1890, leg. Catat, 1 immature ♂ holotype (MNHN CB019).

Z. pygidiale: Madagascar, côte est, XII.1872, leg. Grandidier, 1 ♂ lectotype (here designated) (MNHN CB043); same data as lectotype, 3 ♂♂, 2 ♀♀, 2 ♀♀ (broken) paralectotypes (MNHN CB043). — Antananarivo, 1890, leg. Catat, 1 ♂ paralectotype (MNHN CB043).

OTHER MATERIAL EXAMINED. — **Madagascar**. No locality data, 1957, leg. Demange, 9 ♀♀ (some broken), determined as *Z. anale* (MNHN CB008). — Antananarivo

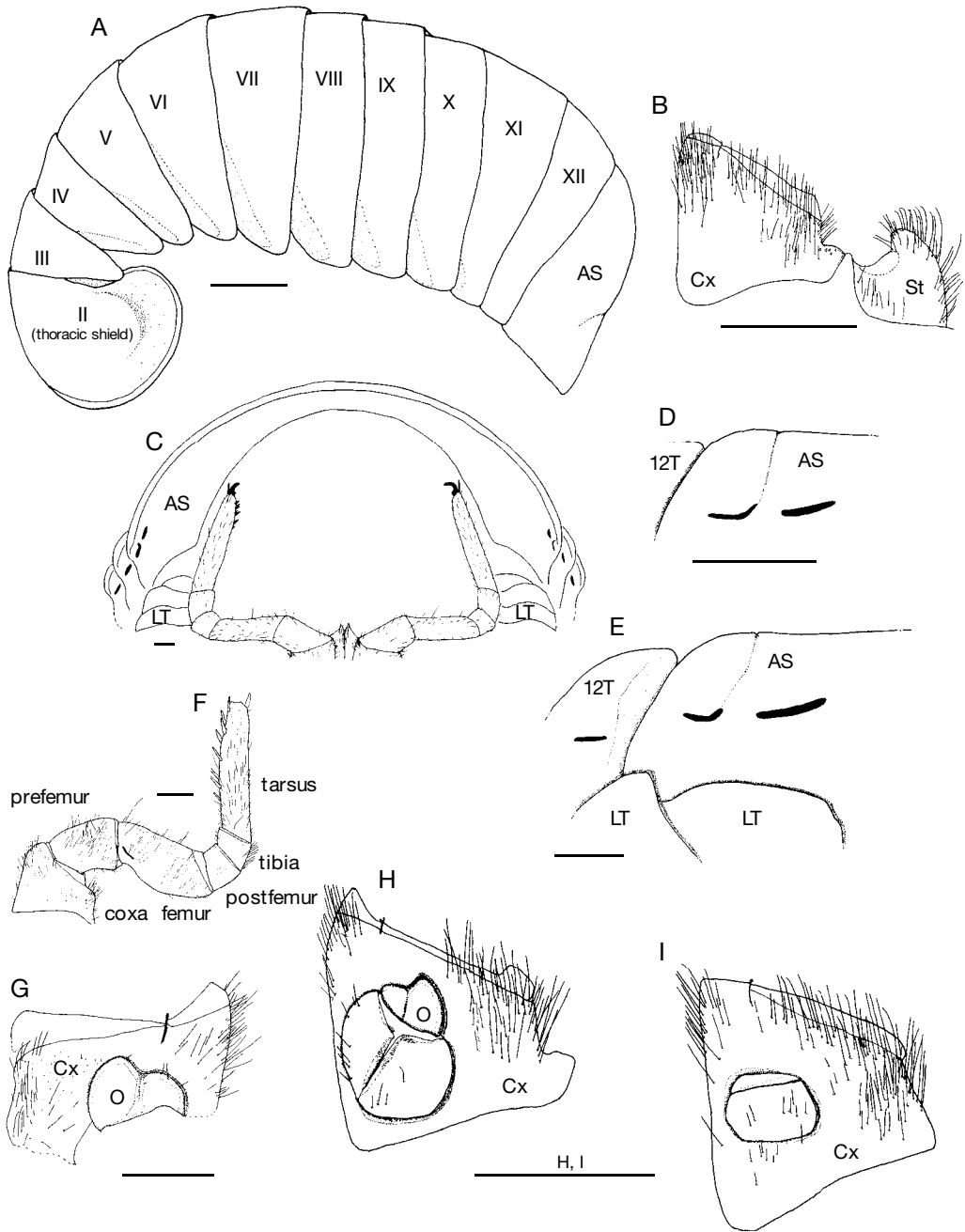


FIG. 1. — *Zoosphaerium neptunus* (Butler, 1872): **A–C** ♂ (MNHN CB020); **A**, habitus; **B**, coxa of 1st left leg with 1st stigma-carrying plate; **C**, posterior body end with anal shield, ventral view, last three leg pairs and telopods removed; **D**, closing ledges of anal shield (holotype of *Z. digitale* n. syn.); **E**, closing ledges of anal shield (lectotype of *Z. pygidiale* n. syn.); **F**, **G**, holotype; **F**, 9th left leg; **G**, operculum of vulva; **H**, coxa of 2nd left leg with vulva (paralectotype of *Z. pygidiale* n. syn.); **I**, coxa of 2nd left leg with gonopore (MNHN CB020). Abbreviations: 12T, 12th tergite; AS, anal shield; Cx, coxa; LT, laterotergite; O, operculum; St, stigma-carrying plate. Scale bars: A, 10 mm; B–I, 1 mm.

(environs), leg. Lamberton (Acad. malgache), 3 ♂♂, 7 ♀♀ (MNHN CB020). — Moramanga, 7.XI.1897, coll. Broelemann, 1 ♂, 1 ♀ (MNHN n° 14). — Reg. de Fenerive, env. de Soanivra, 1909, A. Mathiaux, 4 ♂♂, 6 ♀♀ (MNHN n° 28a). — No locality data, coll. Oberthur, 11 ♀♀ (MNHN n° 34). — Fanovana (forêt de l'est), 9.VII.1942, leg. R. Decary, 7 ♂♂, 7 ♀♀ (MNHN n° 77b). — P[?] de Moramanga, forêt de Manambato, 1927, leg. G. Petit, 1 ♂, 1 ♀ (MNHN n° 122). — No locality data, leg. Alluaud, 1 ♀ (MNHN n° 125). — Forêt parallèle à la côte est, dite forêt de l'Ankaye, P[?] De village d'Analamalotra, 3. juil. 1894, leg. M. H. Guinard (172-94), 2 ♀♀ (MNHN n° 128). — Anderorante, 1899, leg. Mathiaux, 4 ♂♂, 3 ♀♀ (MNHN n° 131). — No locality data, leg. le Corre, 1985, 7 ♀♀ (MNHN n° 132a). — Zahamena, en forêt, 22.III.1941, leg. R. Decary, 2 ♀♀ (MNHN n° 135). — Montagne d'Ambre, montane rainforest, coll. S. Goodman, 1 ♀ (FMMC 3924). — Forêt de Betaolana, along Ambolokopatrika river, 8.5 km NW Ambodiangezoka, 14°32.3'S, 49°26.3'E, 875 m, pitfall, 8-13.XI.1999, coll. S. Goodman, 1 ♀ (FMMC 5440). — Parc national de Marojejy, 450 m, coll. S. Goodman, 2 ♀♀ (FMMC 7856). — 450 m, coll. S. Goodman, 2 ♀♀ (FMMC 7859). — Manantenina River, 775 m, 27.6 km 35°NE Andapa, 9.6 km 327°NNW Manantenina, rainforest, 14°26'06"S, 049°45'36"E, 15-18.XI.2003, coll. B. L. Fisher *et al.*, general collecting, 3 ♀♀ (BLF 8874). Life observation: Perinet.

DIAGNOSIS. — Females gigantic, up to 80.9 mm long. Males smaller, up to 45.5 mm with bell-shaped anal shield. Colour green, varying between shiny light green to olive-greenish (Fig. 5A). Surface of tergites smooth and glabrous. Joints 1-5 of antenna with sclerotized teeth. Apical joint with 18-26 sensory cones. All antennal joints without groove (Fig. 3A-C). Third joint of posterior telopods long, straight, gradually becoming more slender towards its stout ending tip (Fig. 2F-I). Last joint of anterior telopods without cavity but with 3 or 4 spines and covered with numerous sclerotized teeth (Fig. 2A-E). Single stridulation rib on each male harp (Fig. 2C). Anal shield in males bell-shaped (Fig. 1A). Two well-developed, black locking carinae on each side of anal shield, posterior carina short, almost of same size as anterior carina (Fig. 1C, D). Operculum of vulva apically with 2 well-rounded tips, lateral tip protruding twice as high as internal one (Fig. 1G, H).

SIMILAR SPECIES

Only *Z. campanulatum* shows similarly shaped telopods, but it is clearly distinguishable by the shape of the posterior telopods, a different endotergum pattern and a more bell-shaped (weakly bell-shaped in *Z. neptunus*) anal shield. Females of *Z. neptunus*

are distinguishable from congeners by the unique shape of the operculum and the two small locking carinae on the anal shield.

DESCRIPTION

Body measurements: males (12 specimens): length up to 45.5, width of thoracic shield up to 21.5, height of thoracic shield up to 11.35. Females (numerous specimens): length up to 80.9, width up to 45.85.

Habitus: gigantic species, tergites smooth and hairless.

Coloration: tergites green, posterior margin with thin brown line. Head, antennae and legs also greenish. Preserved specimens darken in alcohol, becoming light brown.

Head: more than 80 ocelli.

Antennae: length of joints: 1<2>3>4<5<<6 (Fig. 3A, B), sixth joint longest, of cylindrical shape (Fig. 3B), on tip bearing a disc with 18-26 sensory cones (Fig. 3C). Tip of sensory cones with numerous tube-like structures (Fig. 3D). First joint remarkably broader than others (Fig. 3A), but short and without groove (Fig. 3A). Sclerotized teeth at base of joints 1-3, reaching apical border only on first joint (Fig. 3A).

Mandible: with 6 rows of pectinate lamellae, number of teeth decreasing proximad (Fig. 4B). Condylus with single, strongly developed step near apical margin (Fig. 4B).

Gnathochilarium: ventral side with numerous bristles. Four sensory cones located together lateral of palpi (Fig. 4A). Sensory cones on tip of palpi forming 1 cluster, vale on backside without sensory cones (Fig. 4A). Sensory uvulae on central pads not visible.

Collum: anterior margin with long, isolated hairs arranged in 2 rows, posterior margin with 1 row of even more strongly isolated hairs, edges with up to 5 long hairs. Remaining part of collum glabrous.

Thoracic shield (enlarged 2nd tergite = Brustschild *sensu* Verhoeff 1928: 473): with few hairs in concave lateral extension ("Brustschildgruben") of thoracic shield, particular, located at margins (Fig. 1A).

Tergites: tips of posterior margins of paratergites slightly projecting posteriorly. Tergites smooth and glabrous.

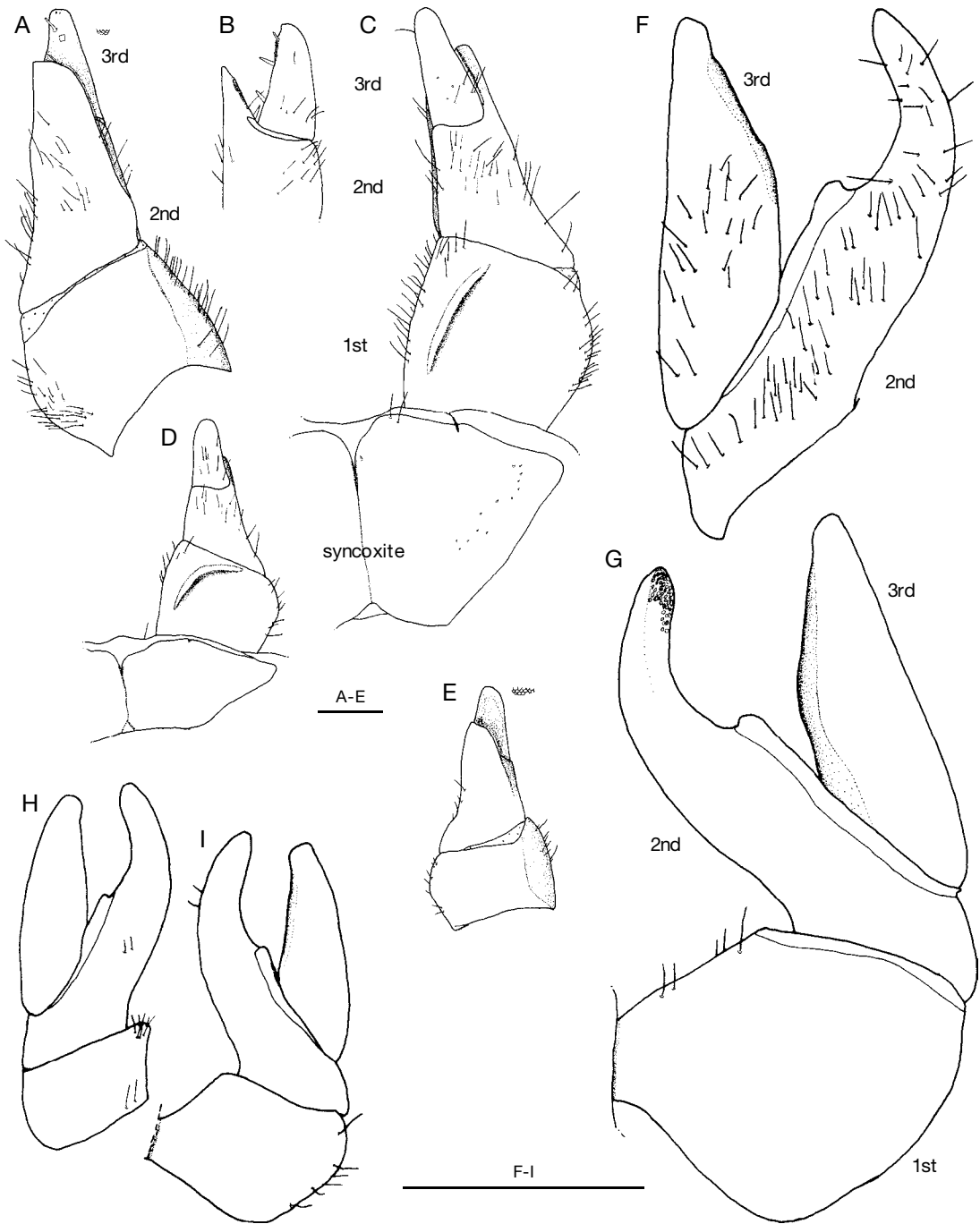


FIG. 2. — *Zoosphaerium neptunus* (Butler, 1872): **A–C**, right anterior telopod (lectotype of *Z. pygidiale* n. syn.); **A**, posterior view; **B**, inner view; **C**, anterior view; **D, E**, right anterior telopod (holotype of *Z. digitale* n. syn.); **D**, anterior view; **E**, posterior view; **F, G**, posterior telopods (lectotype of *Z. pygidiale* n. syn.); **F**, posterior view; **G**, anterior view; **H, I**, posterior telopods (holotype of *Z. digitale* n. syn.); **H**, anterior view; **I**, posterior view. Scale bars: 1 mm.

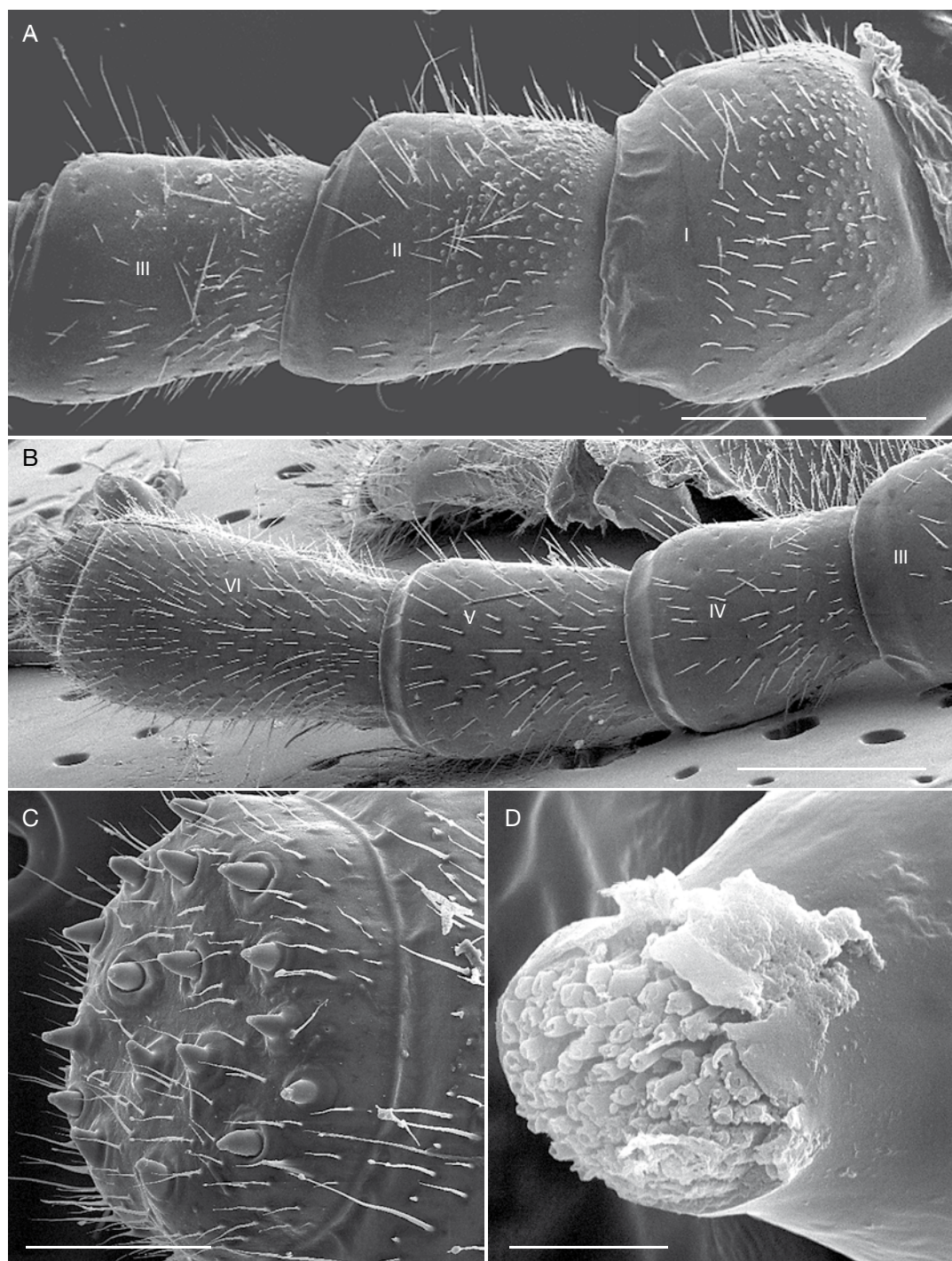


FIG. 3. — *Zoosphaerium neptunus* (Butler, 1872), SEM, right antenna (FMMC 5440): **A**, joints 1-3, lateral view; **B**, joints 4-6, lateral view; **C**, **D**, joint 6; **C**, sensory cones; **D**, tip of sensory cone in detail. Scale bars: A, B, 1 mm; C, 300 µm; D, 8 µm.

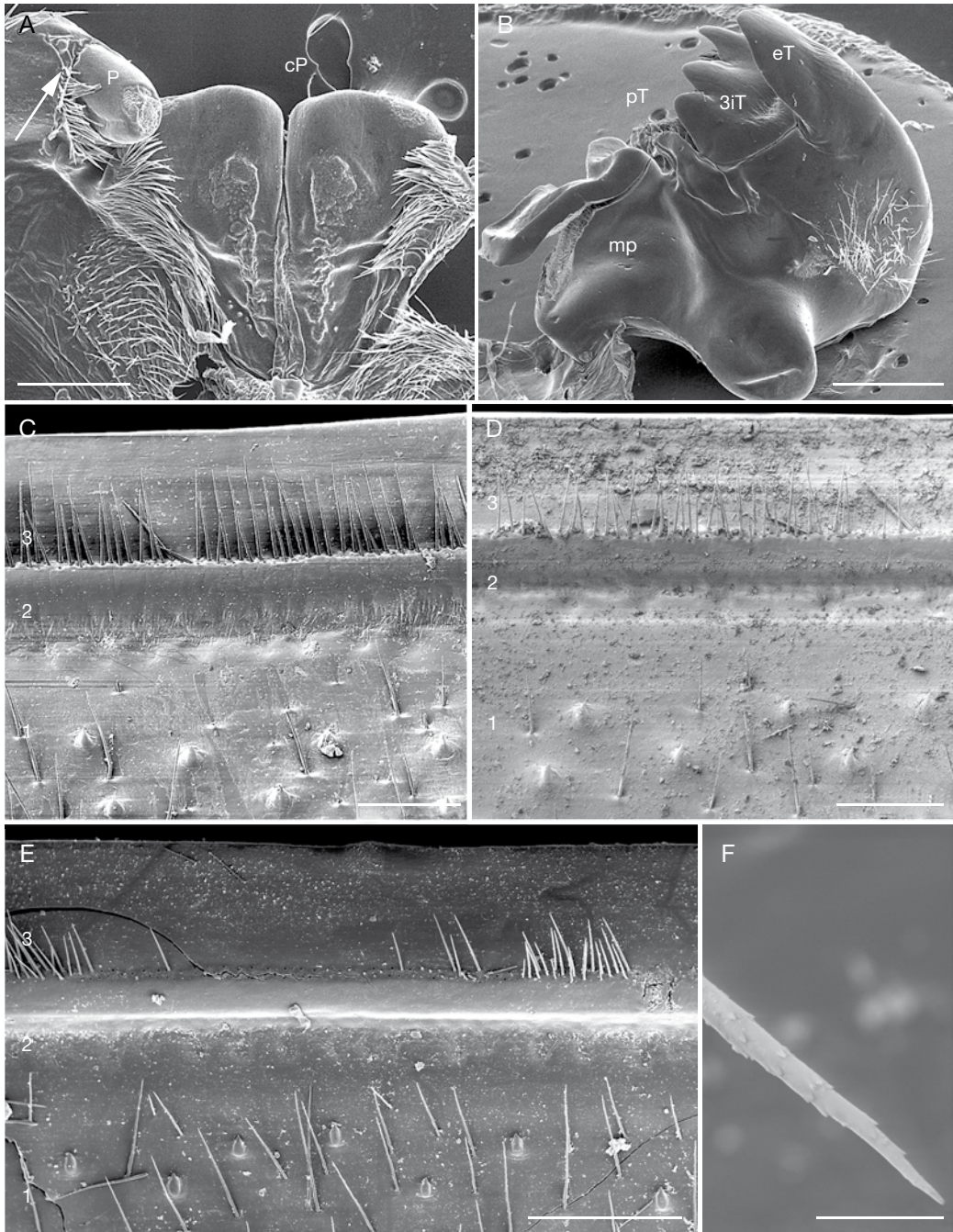


FIG. 4. — *Zoosphaerium neptunus* (Butler, 1872), SEM: **A**, gnathochilarium, posterior view, arrow marks position of lateral sensory cones (FMMC 5440); **B**, right mandible, overview (FMMC 5440); **C–F**, endotergum of midbody tergite; **C**, holotype of *Z. digitale* n. syn.; **D**, lectotype of *Z. pygidiale* n. syn.; **E**, FMMC 5440; **F**, marginal bristle, detail (FMMC 5440). Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section; **3iT**, 3 internal teeth; **cP**, central pads; **eT**, external tooth; **mp**, molar plate; **P**, palpus; **pT**, pectinate lamella. Scale bars: A, 500 μ m; B, 1 mm; C, D, 200 μ m; E, 400 μ m; F, 10 μ m.

Endotergum: internal section with short spines and few isolated bristles. One row of rounded cuticular patterns between marginal ridge and inner area, distance between patterns shorter than their diameter (Fig. 4C-E). Externally two rows of marginal bristles, placed close to one another. Bristles scaly (Fig. 4F), protruding up to 1/2-2/3 towards the area between basis of bristles and posterior end of endotergum (Fig. 4E).

Anal shield: in males strongly, in small females weakly bell-shaped (Fig. 1A). In contrast to glabrous tergites in males covered laterally with numerous, small, round pits, some of which support a short hair. Ventral side carrying 2 black locking carinae on both sides, both similar to those of tergites, posterior carina of same size as anterior one, both carinae running almost parallel to margin. Locking carinae separated from each other by a distance equal to or even longer than shorter carina. A distinct suture between both carinae, representing border of 13th tergite fused to anal shield (Fig. 1C-E).

Legs: first tarsi with 3-6, second with 5-7, third with 6-8 ventral spines. First two leg pairs with only weakly curved claws, without apical spine. Tarsi 4-21 4.6 times longer than wide, with curved claws, 8-10 ventral spines and one apical spine. All femora with short crenulated ridge (Fig. 1F).

Stigma-carrying plates: first stigma-carrying plate lobe short, not protruding above apical edge of coxa 1, covered with long hairs and curved towards the coxa (Fig. 1B). Lobe short with slender rounded tip (Fig. 1B).

Female sexual characters: subanal plate with a washboard consisting of well-developed stridulation ribs, 2 up to 3 ribs on each side. Stridulation ribs asymmetrical and of varying length. Vulva large, covering more than 2/3 of coxa (Fig. 1H). Operculum elongated, protruding up to apical edge of coxa. Apical margin of operculum medially notched (subreniform), with 2 rounded tips. Lateral tip protruding twice as high as inner tip (Fig. 1H). Space between the tips notched, dividing operculum into 2 differently sized parts (Fig. 1G). Inner and exterior plates long and broad, surrounding base of operculum.

Male sexual characters: male gonopore covered with single, large, sclerotized, undivided and rounded

plate. Apical part of plate membranous. Gonopore covering 1/3 of coxal height and 1/2 of its width (Fig. 1I). Anal shield bell-shaped and covered with numerous round pits. Males reach only half the body size of females

Anterior telopods: first joint with a stridulation harp and one stridulation rib. Rib running from basal to apical margin of first joint almost straight, only in younger males curved (Fig. 2C, D). Second joint process reaching 1/2-3/5 of third joint's height. Process towards third joint with sclerotized spots and 1 sclerotized spine (Fig. 2B). Third joint becoming slimmer towards tip, apical margin well-rounded. Posterior side without cavity, completely covered with sclerotized teeth and 3 long spines (Fig. 2A, E). Syncoxite of anterior telopods on both sides with neither hair nor spines. First joint only at margins with some isolated hairs, second joint on both sides with few isolated hairs, third joint glabrous (Fig. 2A, C).

Posterior telopods: third joint becoming slimmer towards tip. Joint with a lower area, in which sclerotized teeth, spots, spines or lobes are absent. Process of second joint with strongly arched tip. Anterior side without spines, apically with some sclerotized spots juxtaposed to lower part of third joint. Chela on anterior side with few isolated hairs, posterior side completely covered with isolated long hairs. Membrane between second and third joint prolonged into a short, stout membranous lobe (Fig. 2F-I). First joint basally with some small hairs. Inner horns with sharp tip, posteriorly weakly curved, laterally straight.

INTRASPECIFIC VARIATION

Body length of females is significantly higher than in males.

DISTRIBUTION AND ECOLOGY

This species is widely distributed. It has hitherto been recorded from 12 localities, all in rainforests (Fig. 6), mostly in the northern half of the island. Elevation ranges from lowland forests up to 850 m. In this species, such an unusual behaviour as mass occurrences (Fig. 5C) has been observed in the field (Prof. v. Tschirnhaus pers. comm. 2004, 2006). Such mass occurrences have never been reported before



FIG. 5. — **A**, *Zoosphaerium neptunus* (Butler, 1872), photograph of living animal; **B**, *Z. libidinosum* (de Saussure & Zehntner, 1897), ♀ (FMNH 5409); **C**, *Z. neptunus*, mass occurrence at Marojej 2006. C photograph by Nils Hasenbein, all rights reserved.

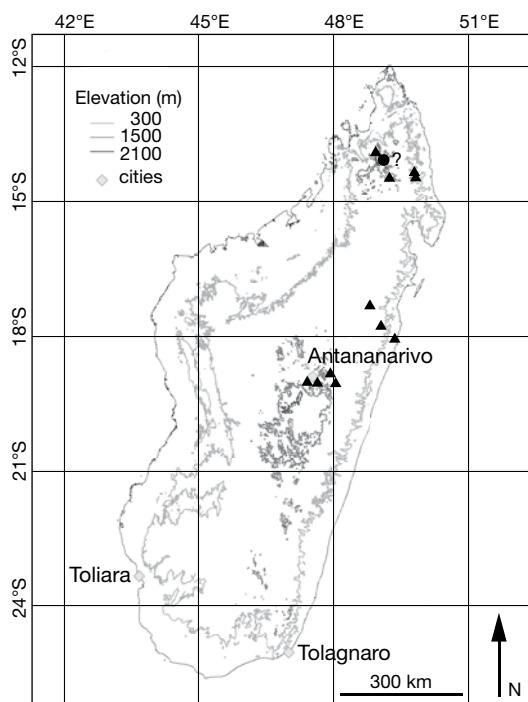


FIG. 6. — Distribution map of *Zoosphaerium neptunus* (Butler, 1872) (▲) and *Z. campanulatum* (de Saussure & Zehntner, 1897) (●).

in the entire order Sphaerotheriida, although in some other groups of millipedes, mainly those of the order Julida, many reports exist from all over the world (see Voigtländer 2006 for an overview). The causes for such an unusual behaviour are little understood. Nevertheless, those mass occurrences have resulted in one of the most serious human-millipede conflicts, leading to attacked houses (Voigtländer 2006) and even derailed trains (Verhoeff 1900), possibly only surpassed by the roof-eating behavior of some diplopods in India (Alagesan & Muthukrishnan 2006).

CONSERVATION

Because of the wide distribution on Madagascar and the occurrence of this species in some protected areas, *Z. neptunus* does not seem to be under a threat of extinction. Nevertheless, it can be concluded that this species has lost most parts of its former distribution area, because its habitat, the eastern

lowland forest and center elevation forest, has been destroyed in most part of the island (Dufils 2003). Furthermore, *Z. neptunus* is an important part of pet trade. It can frequently be found in terraristic shops in Western Europe and the USA. Males are rare in collections, as was also documented in *Z. arborealis* Wesener & Sierwald, 2005. Possibly the collectors focused on the larger females.

REMARKS

The type of the insufficiently described *Z. neptunus* was not reinvestigated by de Saussure & Zehntner when they described *S. digitale* and *S. pygidiale* in 1897 (descriptions completed in 1902). De Saussure & Zehntner (1902) even presented a drawing of the vulva of *Z. neptunus* as a redescription of *S. hippocastanum* (Gervais, 1847). The description of *S. digitale* was based on a small, immature single male specimen. De Saussure and Zehntner observed the striking similarity in the telopods of *S. digitale* and *S. pygidiale*, they nevertheless did not hesitate to separate them because *S. digitale* was smaller and the third joint of posterior telopods in *S. pygidiale* had a blunt ending. Examination of the type series of *S. pygidiale* showed that this observation was not correct: in one male of the type series, the right telopod shows this blunt ending, but the left telopod of the same specimen and furthermore those of the other males in the type series do not show this character (Fig. 2F, G). In fact, their telopods are shaped like those of the holotype in *S. digitale* (Fig. 2H, I). Brolemann redescribed *S. digitale* in 1922, but he did not study the type of *Z. neptunus*. He did not mention the description of the genus *Zoosphaerium* Pocock, 1895 when he erected the subgenus *Globotherium*, with *Sphaerotherium digitale* as type species. Brolemann did not compare *S. digitale* with *S. pygidiale*. The fact that *Sphaerotherium digitale* is identical to *Zoosphaerium neptunus* was observed while studying large samples. In one sample there were differently sized females, smaller females with vulvae like those of *S. digitale* (Fig. 1H) and larger ones with vulvae like those of *Z. neptunus* (Fig. 1G). This sample did also include males, which were identical to the types of *S. digitale* and *S. pygidiale*. Directly comparing the types of all three species showed a

striking similarity in all observed characters, including the endotergum. Because of this observation, *S. digitale* de Saussure & Zehntner, 1897 and *S. pygidiale* de Saussure & Zehntner, 1897 are presented as synonyms of *Zoosphaerium neptunus*. Furthermore, because *S. digitale* is the type species of the subgenus *Globotherium* Brolemann, 1922 while *Z. neptunus* is the type species of the genus *Zoosphaerium*, *Globotherium* is a subjective junior synonym of *Zoosphaerium*.

Zoosphaerium campanulatum
(de Saussure & Zehntner, 1897)
(Figs 7; 8)

Sphaerotherium campanulatum de Saussure & Zehntner, 1897: pl. 4, figs 6-6b; 1902: 28. — Attems 1910: 15 (lists species name, locality east Madagascar, Sakana).

Zoosphaerium campanulatum – Jeekel 1999: 9 (lists species name). — Enghoff 2003: 620 (lists species name).

HOLOTYPE. — ♂ (MNHN CB013).

TYPE LOCALITY. — Madagascar, côte sud-ouest, leg. Grandidier.

OTHER MATERIAL EXAMINED. — **Madagascar.** 1902, coll. Broelemann, Dollfus?, 1 ♂ (MNHN n° 10).

DIAGNOSIS. — Medium sized giant pill-millipede. In alcohol brownish, tergites at posterior margin darker brown. Surface of tergites smooth and glabrous. First antennomere without groove but with sclerotized teeth. Third joint of posterior telopods remarkably thick and with stout, broad tip (Fig. 7G, H). One stridulation rib on each male harp (Fig. 7F). Third joint of anterior telopods without a cavity or visible spines and lobes, but covered with numerous sclerotized teeth (Fig. 7E). Anal shield strongly bell-shaped (Fig. 7D). Two well-developed, black locking carinae on each side of the anal shield, posterior carina short, only 1.5 times longer than anterior carina (Fig. 7B). Females unknown.

SIMILAR SPECIES

Only *Z. neptunus* has similarly shaped telopods, but *Z. campanulatum* is clearly distinguishable by the stout appearance of posterior telopods (sharper in *Z. neptunus*), different endotergum pattern and a strongly bell-shaped (weaker bell-shaped in *Z. neptunus*) anal shield.

DESCRIPTION

Body measurements (male holotype): width of thoracic shield up to 25.5, height of thoracic shield up to 13.3.

Habitus: anal shield bell-shaped (Fig. 7D). Tergites smooth and glabrous.

Coloration: tergites (in alcohol) light brownish, posterior margin with thin darker brown line. Antennae and eyes green.

Head: posterior margin of head towards collum with patch of small hairs. Eyes with more than 80 ocelli.

Antennae: sixth joint longest, of cylindrical shape, with 31-33 sensory cones. First joint cylindrical, broader than the others without groove. Sclerotized teeth present, reaching up to apical border.

Collum: only anterior and posterior margin with some long, isolated hairs.

Thoracic shield: surface similar to those of other tergites.

Tergites: tergites smooth and glabrous.

Endotergum: internal section with short spines and few, isolated bristles (Fig. 8). A single row of barely visible, rounded cuticular patterns present between marginal ridge and internal area. Externally 2 rows of marginal bristles placed close to one another. Bristles reaching up to posterior end of endotergum (Fig. 8).

Anal shield: strongly bell-shaped (Fig. 7D). In contrast to glabrous tergites covered laterally with numerous small round pits, supporting short hairs. Ventral side carrying 2 black locking carinae on both sides, anterior one similar to those of tergites, posterior carina of same size as anterior one, both carinae running parallel to margin. Locking carinae separated from each other by a distance equal to length of shorter carina. A distinct suture between both carinae, representing border of 13th tergite fused to anal shield (Fig. 7B).

Legs: first tarsi with six ventral spines, weakly curved claws and without apical spine. Tarsi 3-21 4.7 times longer than wide, with small, curved claws, 9-11 ventral spines and one apical spine (Fig. 7A). All femora with long crenulated ridge (Fig. 7A).

Stigma-carrying plate: first stigma-carrying plate lobe short, not protruding above coxa 1, covered with long hairs and curved towards coxa (Fig. 7C).

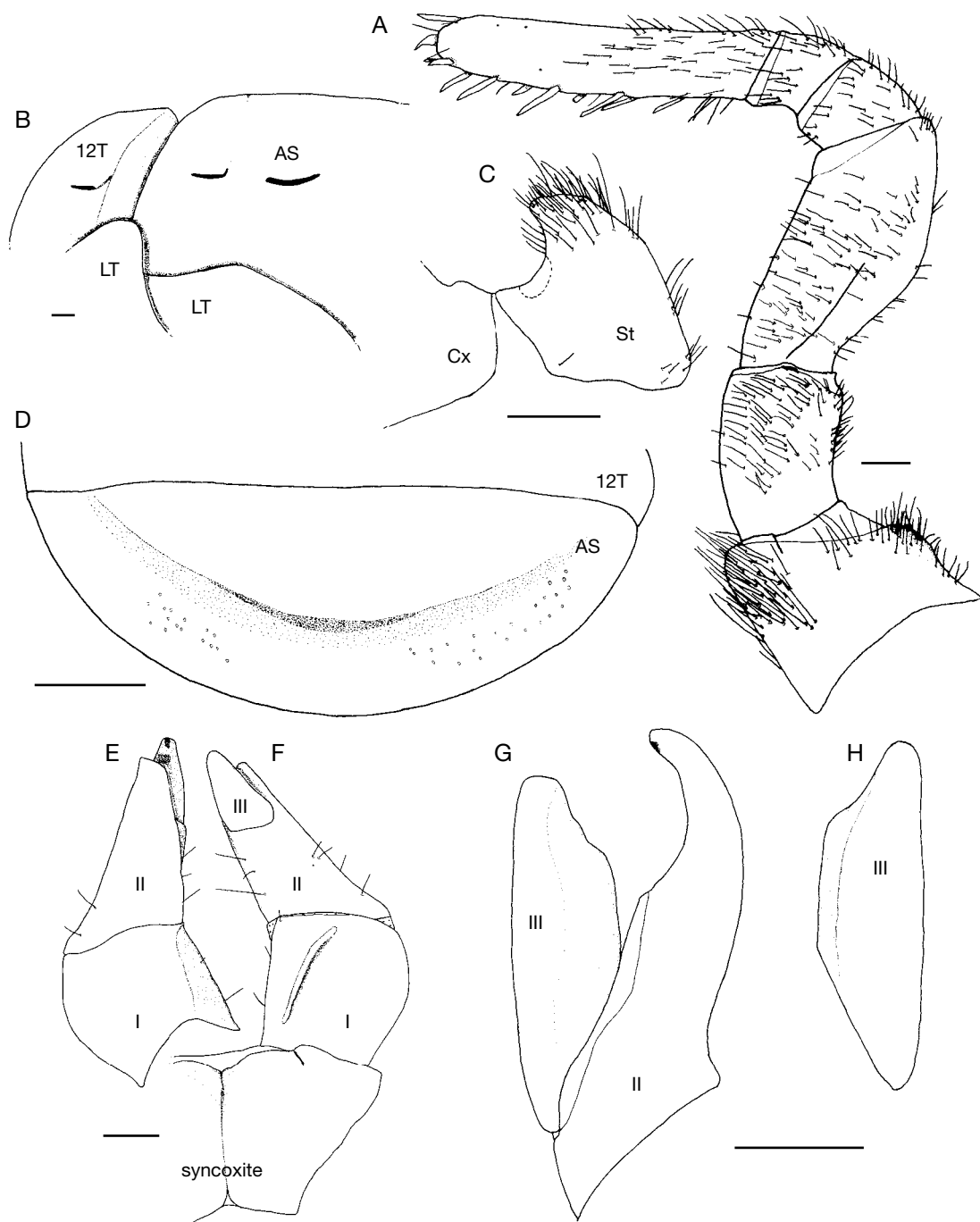


FIG. 7. — *Zoosphaerium campanulatum* (de Saussure & Zehntner, 1897), holotype: **A**, 10th left leg; **B**, closing ledges of anal shield; **C**, coxa of 1st left leg with stigma-carrying plate; **D**, anal shield, dorsal view; **E**, **F**, right anterior telopod; **E**, posterior view; **F**, anterior view; **G**, **H**, left posterior telopod; **G**, 2nd and 3rd joints, anterior view; **H**, 3rd joint, posterior view. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **LT**, laterotergite; **St**, stigma-carrying plate. Scale bars: A-C, 1 mm; D, 5 mm; E-H, 1 mm.

Lobe with slender and rounded tip (Fig. 7C). Female unknown

Male sexual characters: anal shield bell-shaped (Fig. 7D).

Anterior telopods: first joint with a stridulation harp and one straight stridulation rib (Fig. 7F). Second joint process towards third joint with sclerotized spots, protruding up to 3/5 of third joint's height. Apical margin of third joint well-rounded, slimmer towards tip. Posterior side of third joint without a cavity, completely covered with sclerotized teeth (Fig. 7E). Syncoxite of anterior telopods on both sides without hair. Margins of first joint depression laterally with few, isolated hairs, otherwise glabrous. Second joint on both sides at margins with few isolated, long hairs.

Posterior telopods: third joint of chela especially on basal 2/3 of its length greatly enlarged, tip stout (Fig. 7G). Third joint lower area wide, without any sclerotized teeth, spots, spines or lobes. Process of second joint arched towards third joint. Anterior side without spine, apically with some sclerotized spots juxtaposed to lower part of third joint. Chela glabrous (Fig. 7G, H). First joint basally with some small hairs.

INTRASPECIFIC VARIATION

Too few specimens are known to evaluate the intraspecific variation. Body, particularly anal shield, covered with long, black, irregular scars which are 3–10 mm long and 1–3 mm wide.

DISTRIBUTION AND ECOLOGY

This species seems to be collected in hylaea forests, but no precise location dates are given. Furthermore this species is not present in recent collections of the CAS or FMNH. Distribution is indicated in Figure 6.

CONSERVATION

All known collection dates of this species are more than 100 years old. It is unknown if this species still exists.

Zoosphaerium libidinosum species-group

SPECIES INCLUDED. — *Zoosphaerium libidinosum* (de

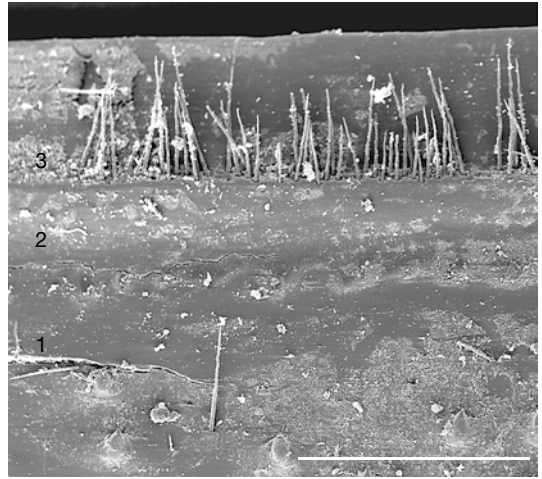


FIG. 8. — *Zoosphaerium campanulatum* (de Saussure & Zehntner, 1897), SEM, holotype, endotergum of midbody tergite, overview. Abbreviations: 1, endotergum, internal section; 2, endotergum, medial section; 3, endotergum, external section. Scale bar: 300 μ m.

Saussure & Zehntner, 1897); *Z. arborealis* Wesener & Sierwald, 2005; *Z. lambertoni* (Brolemann, 1922); *Z. priapus* (de Saussure & Zehntner, 1897); *Z. anomalum* (de Saussure & Zehntner, 1902).

DIAGNOSIS. — These Malagasy giant pill-millipede species share a number of characters, identifying them as a species-group. Species of this group can be identified by a striking similarity in the shape of posterior telopods (Figs 9K; 14K; 17I). The third joint carries always more than 15 large, sclerotized, crenulated teeth on its backside closely to the tip. The hollowed-out margin juxtaposed to the second joint carries 2 large, membranous lobes and some shorter sclerotized spines (Figs 9K; 14L; 17J). To this species-group belong the only *Zoosphaerium* taxa, which (still?) possess a well-rounded operculum (Fig. 9C, D). Inside the group the species are clearly distinguishable by numerous characters, like the shape of anterior pair of telopods, the number of sensory cones on antenna, sensory cones on gnathochilarium, special shape of the female vulva operculum, body size, special bristle patterns on the collum and different structures on the surface of tergites.

REMARKS

A phylogenetic analysis will be necessary to confirm if the *libidinosum*-group represents a monophyletic group to be kept separately from the other Malagasy sphaerotheriids.

KEY TO THE *ZOOSPHAERIUM LIBIDINOSUM* SPECIES-GROUP

1. Inner margin of anal shield without locking carinae (in small, immature individuals traces of carinae can be visible). Operculum of female vulva well-rounded, not notched (Fig. 10C). Tarsi slim, antenna with more than 10 sensory cones. Adults > 25 mm ... *Z. libidinosum*
 — Inner margin of anal shield with 2 well-visible locking carinae (Fig. 14C). Apical margin of vulva operculum medially notched (Fig. 14D) 2
2. Hindmost point of anal shield extended, slightly protruding posteriorly 3
 — Hindmost end of anal shield well-rounded 4
3. Posterior locking carina of anal shield more than 3 times longer than anterior carina *Z. arborealis*
 — Posterior locking carina less than 3 times longer than anterior one *Z. lambertoni*
4. Brown-blackish coloration pattern. More than 10 sensorial cones on antenna (Fig. 15C). Legs short, covered with long hairs (Fig. 14B). Third joint of posterior telopods without small hairs, second joint basally with one large, membranous lobe (Fig. 14K) ... *Z. priapus*
 — Shiny green coloration pattern (Fig. 6A). Four sensorial cones on antenna. Legs elongated. Second and third joints of posterior telopods covered with numerous minute hairs. Process of second joint basally without membranous lobe (Fig. 17I, J) *Z. anomalum*

Zoosphaerium libidinosum
 (de Saussure & Zehntner, 1897)
 (Figs 9-11)

Sphaerotherium libidinosum de Saussure & Zehntner, 1897: pl. 4, fig. 2-2i; 1901: 435; 1902: 69, pl. 15, fig. 2. — Attems 1910 (lists species name).

Sphaerotherium (Globotherium) libidinosum – Demange 1969: 485.

Zoosphaerium libidinosum – Jeekel 1999: 12 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — Madagascar, leg. Grandidier, ♂ lectotype (here designated) (MNHN CB034). — Same data as lectotype, 5 ♂♂ paralectotypes (MNHN CB034); 1 ♂, 8 ♀♀ (MNHN CB035). — Leg. Grandidier n° 217, 1 ♂, 1 ♀, (MNHN CB036).

TYPE LOCALITY. — Madagascar.

OTHER MATERIAL EXAMINED. — **Madagascar.** No locality data, leg. Coquerel 1862, 2 ♂♂ (MNHN CB037). — Tuléar, bush, coll. Bigot, 19.IV.1965, 1 ♀ (MNHN CB037). — Forêt d'Elakilaka, 1901, coll. C. Alluaud, 1 ♀ (MNHN n° 16). — Environ de Tuléar, 30.V.1898, leg. G. Grandidier, 1 ♀ (MNHN n° 19). — Ambovombe, sur le sol, en forêt broussailleuse, 27.II.1931, coll. Mission R. Decary, 1 ♂ (MNHN n° 41). — Région de sakarami, 1909, coll. M. de Rothschild, 1 ♂ (MNHN n° 56). — Pays Mahafaly, 1900, leg. Bastard, 1 ♂, 1 ♀ (MNHN n° 71). — Env. Tuléar, coll. Prod'hon J., leg.

Albaret, 1972, 2 ♂♂ (MNHN n° 78). — Beloka (p. de Fort Dauphin), VII.1926, leg. Mission R. Decary, 1 ♀ (MNHN n° 112). — No locality data, leg. G. Petit, entrée 24-1922, 1 ♂, 1 ♀ (MNHN n° 114). — JFP Ihosy (Ranohira-Isalo), I.1962, coll. P. Malzy-Raharizonina, 5 ♀♀ (MNHN n° 115). — Massif de l'Angona, à l'est d'Antanimora (p. de Fort Dauphin), VII.1926, coll. Mission R. Decary, 2 ♂♂, 1 ♀ (MNHN n° 116). — Fort Dauphin, leg. VI.1926, Mission R. Decary, 1 ♂, 5 ♀♀ (MNHN n° 120). — 7.5 km ENE Hazofotsy (Réserve naturelle intégrale d'Andohahela, camp #6), 24°49.0'S, 46°36.6'E, 120 m, pitfall trap, 7-15.XII.1995, coll. S. Goodman, 1 ♂ (FMMC 5369). — Forêt de Vohimena, 35 km SE Sakaraha, 22°41.0'S, 44°49.8'E, 780 m, 17-24.I.1996, coll. S. Goodman, 1 ♂ (FMMC 5395). — 7.5 km ENE Hazofotsy (Réserve naturelle intégrale d'Andohahela, camp #6), 24°49.0'S, 46°36.6'E, pitfall traps 16-18, 120 m, 7-15.XII.1995, coll. S. Goodman, 4 ♂♂, 2 ♀♀ (FMMC 5407); 3 ♀♀ (FMMC 5409). — Forêt des Mikeas, 9.5 km W Ankiloaka, 22°46.7'S, 43°31.4'E, 80 m, pitfall trap, 14-15.II.2003, 1 ♂ (FMMC 5500). — Forêt des Milua, 19 km SW Tanadava, 21°52.0'S, 43°39.6'E, 50 m, pitfall, 16-18.III.2003, coll. S. Goodman, 1 ♂ (FMMC 5680). — Same data as previous, 22-24.III.2003, 2 ♂♂, 1 ♀ (FMMC 5683). — No locality data, coll. S. Goodman, 1 ♀ (FMMC 7827). — Zombitsa NR, 16 km E Sakaraha, trop. forest on sand, 22.88231°S, 44.70062°E, 825 m, 15-18.XII.1999, coll. Schlinger & Irwin, 1 ♀ (CAS Mei-99-MA-14). — Antafoky, 80 m, spiny thicket, 23°29'16"S, 44°4'39"E, 14.XI.2001, coll. Frontier Project, millipede dig (3 m × 3 m), 5 juvs (MGF007). — Antafoky, 50 m, gallery forest, 23°28'23"S,

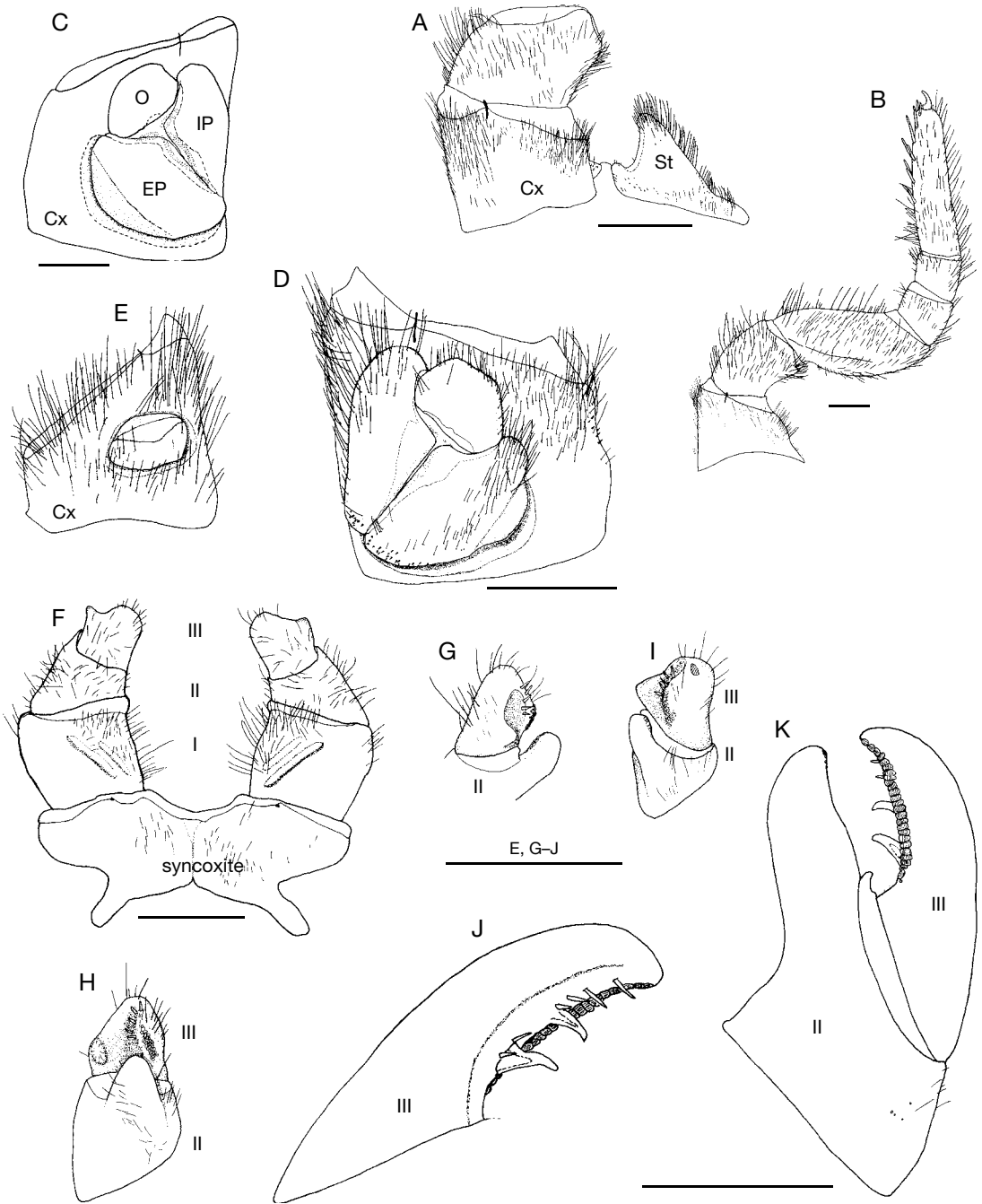


FIG. 9. — *Zoosphaerium libidinosum* (de Saussure & Zehntner, 1897): **A**, coxa of 1st left leg with 1st stigma-carrying plate (BLF 4812); **B**, 9th left leg (BLF 5763); **C**, coxa of 2nd left leg with vulva (BLF 2543); **D**, coxa of 2nd right leg with vulva (BLF MGF029); **E–K** ♂ (BLF 5763); **E**, coxa of 2nd right leg with gonopore; **F**, anterior telopods, anterior view; **G–I**, right anterior telopod; **G**, lateral view; **H**, posterior view; **I**, inner view, left posterior telopod; **J**, joint 3, anterior view; **K**, joints 2 and 3, posterior view. Abbreviations: **Cx**, coxa; **EP**, exterior plate; **IP**, inner plate; **O**, operculum; **St**, stigma-carrying plate. Scale bars: 1 mm.

44°4'19"E, coll. Frontier Project, 10.X.2001, millipede dig (3 m × 3 m), 2 ♂♂ (MGF008). — Antafoky, 60 m, spiny thicket/gallery forest transition, pitfall traps, 23°28'45"S, 44°3'58"E, 1.VII-31.X.2001, coll. Frontier Project, 1 ♂, 6 ♀♀, 3 juvs (MGF009). — Antafoky, 70 m, gallery forest, 23°28'45"S, 44°3'59"E, coll. Frontier Project, 16.X.2001, millipede dig (3 m × 3 m), 1 ♂, 1 ♀ (MGF010). — Forêt de Manantalinjo (Parc national d'Andohahela), 33.6 km 63° ENE Amboasary, 7.6 km 99° E Hazofotsy, spiny forest thicket, 150 m, 24°49'1"S, 46°36'36"E, 12-16.I.2002, coll. Fisher, Griswold *et al.*, general collecting, 1 ♀ (BLF 4812). — Forêt de Mahavelo, Isantoria river, 110 m, spiny forest, 24°45'30"S, 46°9'26"E, 28.I-1.II.2002, coll. Fisher, Griswold *et al.*, pitfall trap, 1 ♂ (BLF 5239). — Same data as previous, general collecting, 1 ♀ (BLF 5241). — Réserve spéciale cap Sainte-Marie, 25°34'54"S, 45°10'6"E, 200 m, spiny forest/thicket, coll. Fisher, Griswold *et al.*, 11-15.II.2002, pitfall trap, 1 ♂, 1 ♀ (BLF 5499). — Same data as previous, general collecting, 1 ♂, 1 ♀ (BLF 5503). — Réserve spéciale cap Sainte-Marie, 160 m, 25°35'40"S, 45°8'49"E, coll. Fisher, Griswold *et al.*, 13-19.II.2002, pitfall trap, in spiny forest/thicket, 1 ♂ (BLF 5650). — Mahafaly Plateau, 6.2 km 74° ENE Itampolo, spiny forest thicket, 80 m, 24°39'13"S, 43°59'48"E, coll. Fisher, 21-25.II.2002, Griswold *et al.*, general collecting, 1 ♂ (BLF 5762). — Same data as previous, pitfall trap, 2 ♂♂ (BLF 5763). — Forêt de Mite, 75 m, 20.7 km 29° WNW Tongobory, 23°31'27"S, 44°7'17"E, gallery forest, 27.II-3.III.2002, coll. Fisher, Griswold *et al.*, general collecting, 1 ♀ (BLF 5851). — Parc national Zombitse, 19.8 km 84° E Sakaraha, 770 m, tropical dry forest, 22°50'36"S, 044°42'36"E, 5-9.II.2003, coll. Fisher, Griswold *et al.*, general collecting, 1 ♂, 1 ♀ (BLF 7509). — Same data as previous, beating low vegetation, 3 ♀♀ (BLF 7511); 1 ♀ (BLF 7512).

DIAGNOSIS. — Up to 33 mm long, both sexes of equal size. Dark-greenish to light green, anterior part of paratergites brownish, tergites at posterior margin brown. Surface of tergites smooth and glabrous. Antennomeres 1-3 with sclerotized teeth, sixth joint with 11-22 sensory cones (Fig. 10B). All antennal joints without groove (Fig. 10A). Third joint of posterior telopods weakly curved, posterior side with more than 20 sclerotized teeth and two large, non sclerotized lobes (Fig. 9K). Two stridulation ribs on male harp (Fig. 9F) and 1-3 on each side of female washboard. Anal shield without locking carinae. Operculum of vulva well-rounded, protruding up to distal end of coxa (Fig. 9C, D).

SIMILAR SPECIES

No other described *Zoosphaerium* species features the complete absence of locking carinae on the anal shield or a well-rounded operculum plus the dense field of long hairs on the endotergum.

DESCRIPTION

Body measurements: males (7 specimens): length up to 32.6, width of thoracic shield up to 16.6, height of thoracic shield up to 8.6. Females (4 specimens): length up to 32.2, width up to 17.2, height up to 10.0.

Habitus: anal shield well-rounded (Fig. 5B). Tergites smooth and glabrous.

Coloration: tergites dark-greenish to light-green, anterior part of paratergites brownish, tergites at posterior margin brown (Fig. 5B). Head, antennae and legs dark green. Preserved specimens lose their coloration pattern in alcohol (Fig. 5B).

Head: posterior margin of head towards collum without patch of small hairs.

Antennae: length of joints: 1>2>3=4=5<6; sixth joint of cylindrical shape (Fig. 10A), on tip bearing a disc with 11-22 sensory cones (Fig. 10B). First joint broadest, short and cylindrical, without groove (Fig. 10A). Sclerotized teeth at base of joints 1-3, reaching apical border only on first joint (Fig. 10A). First joint apically on one side with 1 row of sensilla basiconica (Fig. 10C).

Mandible: with 6 rows of pectinate lamellae; number of teeth decreasing proximad (Fig. 11A).

Gnathochilarium: ventral side with numerous bristles. Lateral of palpi 2 sensory cones located together (Fig. 10D, E). Vale on backside of palpi with some sensory cones. Two different types of sensory uvulae on central pads: long, cylinder-shaped ones with 1 pit in their middle and more plain ones without pit (Fig. 10D, F).

Epipharynx: similar to the shape of other known species of giant pill-millipedes.

Collum: anterior margin with numerous long, isolated hairs arranged in 2 rows, posterior margin with 10-12 hairs, edges with up to 5 long hairs. Remaining parts of collum glabrous.

Thoracic shield: surface structured like those of other tergites.

Tergites: smooth and glabrous. At high magnifications (60 ×) small, dot-like impressions become visible. Tips of posterior paratergites margin slightly projecting posteriorly.

Endotergum: internal section with short spines and few, isolated bristles (Fig. 11B). No cuticular patterns between marginal ridge and internal area (Fig. 11B). Externally more than 3 rows of marginal

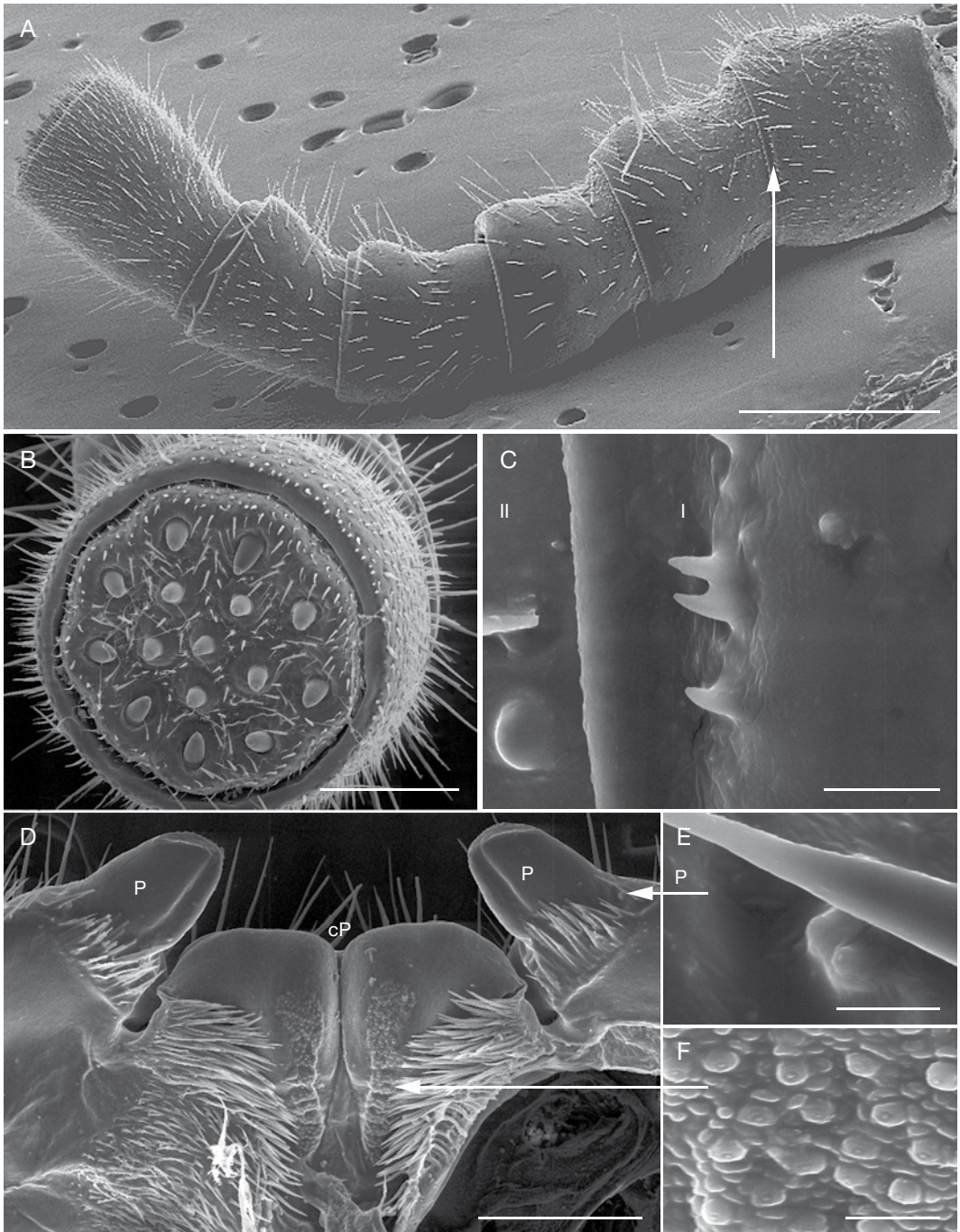


FIG. 10. — *Zoosphaerium libidinosum* (de Saussure & Zehntner, 1897), SEM (BLF 5239): **A–C** right antenna; **A**, overview, lateral view; **B**, joint 6 with disc, apical view; **C**, sensory (?) cones on first joint; **D–F** gnathochilarium; **D**, posterior side; **E**, sensory cone lateral of left palpus; **F**, sensory cones on central located pads. Abbreviations: **cP**, central pads; **P**, palpus. Scale bars: **A**, 1 mm; **B**, 300 μ m; **C**, 30 μ m; **D**, 400 μ m; **E**, **F**, 20 μ m.

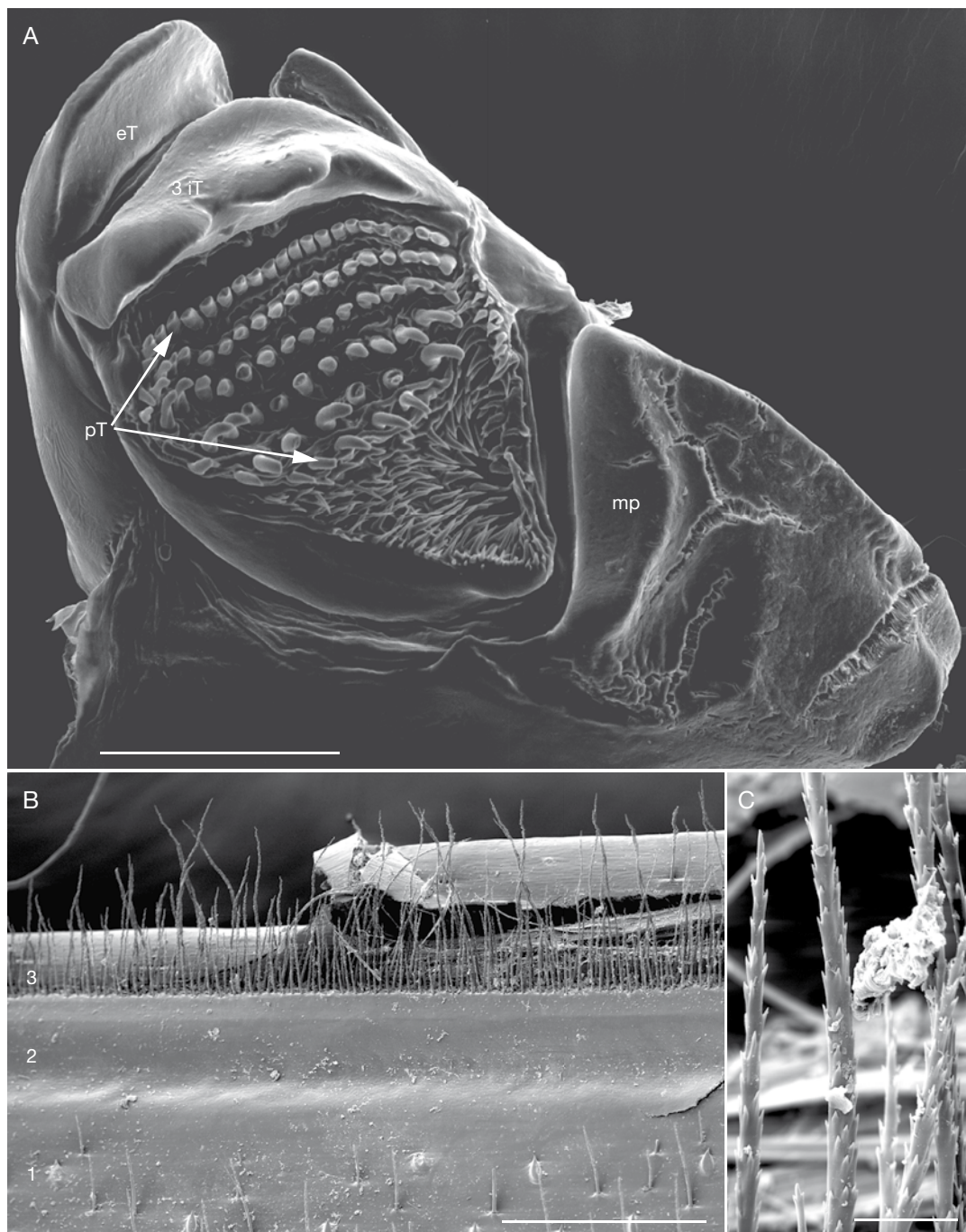


FIG. 11. — *Zoosphaerium libidinosum* (de Saussure & Zehntner, 1897), SEM (BLF5239): **A**, right mandible; **B**, **C**, endotergum; **B**, overview; **C**, marginal bristle, detail. Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section; **3iT**, 3 internal teeth; **eT**, external tooth; **mp**, molar plate; **pT**, pectinate lamella. Scale bars: **A**, 500 µm; **B**, 400 µm; **C**, 10 µm.

bristles, placed close to one another. Bristles scaly (Fig. 11C), long, strongly surmounting posterior end of tergite (Fig. 11B).

Anal shield: rounded, neither bell-shaped nor tapered (Fig. 5B). Ventral side without any trace of locking carinae. No suture present.

Legs: first tarsi with 1 or 2, second with 2-4, third with 3-8 ventral spines. First 2 leg pair with only weakly curved claws and without apical spine. First prefemur with groove. Tarsi 4-21 with curved claws, 11-14 ventral spines and 1 apical spine. Tarsi 3.8 times longer than wide. All femora with crenulated ridge (Fig. 9B).

Stigma-carrying plate: first stigma-carrying plate lobe long, protruding up to apical edge of coxa 1. Lobe weakly curved towards coxa, well-rounded with slim tip (Fig. 9A).

Female sexual characters: subanal plate with a washboard, consisting of well-developed stridulation ribs, 1 up to 3 ribs on each side, depending on female size. Stridulation ribs asymmetrical and weak, ending just above midline of subanal plate. Vulva large, covering more than 2/3 of coxa. Operculum large, protruding up to apical edge of coxa. Apical margin of operculum well-rounded. Inner plate long and broad, protruding up to 1/2 of operculum height. Posterior margins of both inner and exterior plate with short, triangular, black spines (Fig. 9C, D).

Male sexual characters: male gonopore covered with single, large, sclerotized, undivided and rounded plate. Apical (and lateral?) part of plate membranous (Fig. 9E). Anal shield well-rounded.

Anterior telopods: first joint with a stridulation harp and 2 stridulation ribs. Inner rib shorter than lateral one, both ribs straight (Fig. 9F). Second joint towards third joint with sclerotized spots, on posterior side with lobe like, weakly curved process with rounded edges (Fig. 9G-I). Third joint with a cavity juxtaposed to process of second joint. Inner margin of cavity with numerous sclerotized spots and 2 membranous lobes, juxtaposed to sclerotized structures of second joint process. Apical margin of third joint well-rounded, protruding internally higher than laterally. Inner side strongly and lateral side weakly arched towards second joint process (Fig. 9G-I). Syncoxite of anterior telopods on both

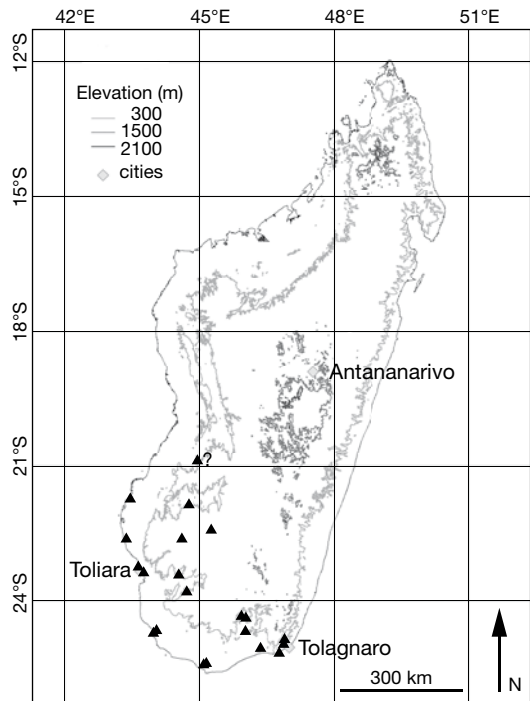


FIG. 12. — Distribution map of *Zoosphaerium libidinosum* (de Saussure & Zehntner, 1897) (▲).

sides with few, isolated hairs (Fig. 9F). Second joint only at margins of depression laterally with 1 row of hairs, otherwise surface glabrous.

Posterior telopods: third joint of chela weakly curved. Hollowed-out margin towards second joint with two non-sclerotized lobes and up to 6 smaller, sclerotized spines (Fig. 9J), on posterior side with *c.* 25 crenulated teeth (Fig. 9K). Process of second joint as wide as third joint, with almost straight tip. Anterior side basally with 1 membranous lobe, apically with few, small, sclerotized spots juxtaposed to third joint (Fig. 9K). Chela only at margins with few isolated hairs, on rest of surface hairs absent. Inner horns of syncoxite with pointed, slender tip arched 40-50°.

INTRASPECIFIC VARIATION

Body length of females not significantly higher than in males. The number of stridulation ribs on female washboard correlates with female size. One

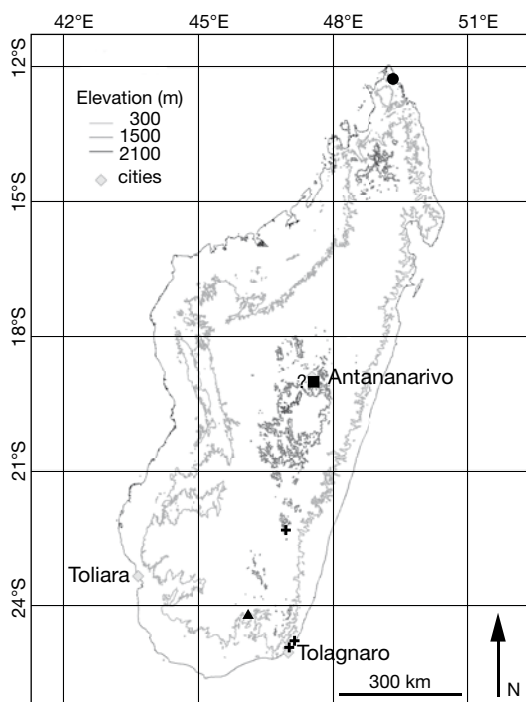


FIG. 13. — Distribution map of *Zoosphaerium arborealis* Wesener & Sierwald, 2005 (+), *Z. lambertoni* (Brolemann, 1922) (■), *Z. priapus* (de Saussure & Zehntner, 1897) (●) and *Z. anomalum* (de Saussure & Zehntner, 1902) (▲).

female among numerous specimens shows a trace of a weakly notched operculum. Some specimens from different locations show little variation in the number of ventral spines on walking legs, displaying nevertheless similar shaped sexual organs. Possibly genetic studies may show if *Z. libidinosum* could include cryptic species.

DISTRIBUTION AND ECOLOGY

This species is one of the few Malagasy giant pill-millipedes with a wide distribution. It was found until now in 17 localities, all located in the southern part of the island (Fig. 12). The ecosystems are gallery forests and spiny forests. *Zoosphaerium libidinosum* was even collected in the driest part of the island, the Mahafaly plateau, and elevation ranges from 50 to 900 m. In fact, *Z. libidinosum* was found in all collection sites of the southern spiny forests. The species was in some areas collected

together with other giant pill-millipede species such as *Zoosphaerium blandum* and *Sphaeromimus musicus*. *Zoosphaerium libidinosum* was mainly collected with hand-collecting methods or using pitfall traps, but at least three young specimens (BLF 7511) were beaten from low vegetation.

CONSERVATION

Because of the wide distribution in one of the least anthropogenically-affected Malagasy ecoregions (Fig. 21), this species seems currently not to be under a threat of extinction.

Zoosphaerium arborealis Wesener & Sierwald, 2005

Zoosphaerium arborealis Wesener & Sierwald, 2005a: 34, figs 19-29.

REMARKS

See Wesener & Sierwald (2005a) for a complete description of this species. No additional material was found in Museum collections.

For distribution, see Figure 13.

Zoosphaerium lambertoni (Brolemann, 1922)

Sphaerotherium (*Globotherium*) *lambertoni* Brolemann, 1922: 235, figs 10-13 (not seen).

Zoosphaerium lambertoni – Jeekel 1999: 13 (lists species name). — Enghoff 2003: 620 (lists species name).

REMARKS

This species seems to be closely related to *Zoosphaerium arborealis*. The type was stored by Brolemann (1922) at the Académie malgache, an institution that does no longer exist. Some of the material of the former Académie malgache is now stored in the zoological collection at Tsimbazawa, Antananarivo, Madagascar. It is unclear, if the holotype and only known individual of *Z. lambertoni* still exists in this collection. Even if it is lost, *Zoosphaerium lambertoni* (Brolemann, 1922) is not listed as a *nomen dubium*, because we have high-quality drawings provided by Brolemann and a locality (“environs de Tanarive”;

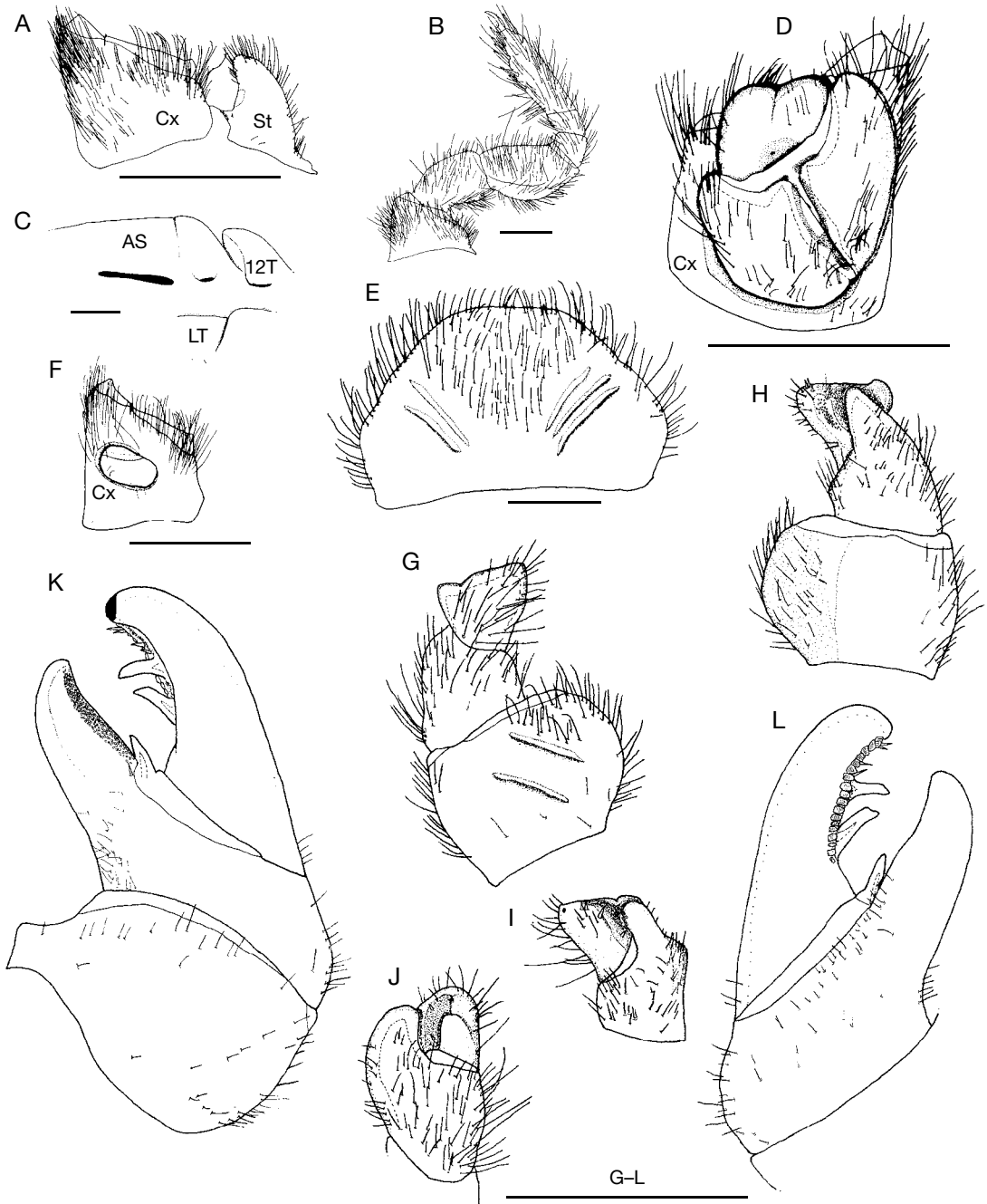


FIG. 14. — *Zoosphaerium priapus* (de Saussure & Zehntner, 1897): **A, B, E**, ♀ (FMNH 3911); **A**, coxa of 1st left leg with 1st stigma-carrying plate, posterior view; **B**, 9th left leg; **E**, subanal plate with washboard; **C, D** lectotype; **C**, closing ledges of anal shield; **D**, coxa of 2nd right leg with vulva; **F-L**, ♂ (FMNH 3911); **F**, coxa of 2nd left leg with gonopore; **G-J** left anterior telopod; **G**, anterior view; **H**, posterior view; **I**, inner view; **J**, lateral view; **K, L** right posterior telopod; **K**, anterior view; **L**, posterior view. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **LT**, laterotergite; **St**, stigma-carrying plate. Scale bars: 1 mm.

Fig. 13), which will perhaps allow the collection and determination of a neotype.

Zoosphaerium priapus
(de Saussure & Zehntner, 1897)
(Figs 14-16)

Sphaerotherium priapus de Saussure & Zehntner, 1897: pl. 4, figs 5-5d; 1902: 61.

Zoosphaerium priapus – Jeekel 1999: 14 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — ♀ lectotype (here designated) (MNHN CB042).

TYPE LOCALITY. — Madagascar, Antananarivo, leg. Catat, 1890.

OTHER MATERIAL EXAMINED. — Forêt d'Orangea, 3.6 km 128° SE Remena, 12°15'32"S, 49°22'29"E, littoral forest, 90 m, pitfall trap, leg. Fisher, Griswold *et al.*, 2 ♂♂, 12 ♀♀, 1 juv. (FMMC 3911); 1 ♀ (FMMC 3922).

DIAGNOSIS. — Up to 30 mm long. Light brownish, posterior margin of tergites and anal shield laterally with black pattern. Surface of tergites smooth and glabrous. Anal shield well-rounded, with rough, leather-like surface, underside carries 2 locking carinae, both short, second even weaker and shorter than first, in some specimens completely absent (Fig. 14C). Antennomeres 1-5 with sclerotized teeth, apical joint with 15-25 sensory cones. All antennal joints without groove (Fig. 14A). Legs short, covered with numerous long hairs (Fig. 14B). First 3 pair of legs without apical spine. Third joint of posterior telopods weakly curved, posterior side with up to 18 sclerotized teeth, two large, non-sclerotized lobes and c. 4 sclerotized spines (Fig. 14K, L). Second joint with broad and stout immovable process and basally with 1 large membranous lobe and a spine. Two stridulation ribs on each male harp and 2-4 on each side of female washboard (Fig. 14E, G). Operculum of vulva large, surmounting coxa, apically with 2 well-rounded lobes protruding to same height (Fig. 14D).

SIMILAR SPECIES

The short and hairy legs, the shape of female operculum and special surface of the anal shield separates *Z. priapus* easily from all other described Malagasy sphaerotheriids.

DESCRIPTION

Body measurements: males (2 specimens): length up to 17.95 (in literature: 25.5 mm, de Saussure &

Zehntner 1902), width of thoracic shield up to 8.8, height of thoracic shield up to 4.9. Females (13 specimens): length up to 30.25, width up to 14.15, height up to 8.05.

Habitus: body high, reaching its highest point at midbody tergites. Tergites smooth and glabrous, at high magnification, small isolate pores and a weak, leather-like surface becomes visible.

Coloration: tergites lightly brown, sometimes brown-reddish, through posterior body end with dark black coloration pattern, becoming much thicker towards tips of paratergites. Posterior end of anal shield dark. Head and collum with dark olive-green to blackish coloration. Antennae and legs olive-greenish. Preserved specimens lose their coloration pattern in alcohol. A nice drawing of the coloration pattern of *Z. priapus* is shown in de Saussure & Zehntner (1897: pl. 4).

Head: posterior margin of head towards collum with patch of small hairs.

Antennae: length of joints: 1>2>3<4=5<6, sixth joint longest, of cylindrical shape (Fig. 15A, C), apically with 1 row of sensilla basiconica, on tip bearing a disc with 15-25 sensory cones (Fig. 15C). Antenna conspicuously short, protruding up to labrum tooth. First joint remarkably broader than others, but short and without groove (Fig. 15A). Sclerotized teeth at the base of joints 1-5, reaching apical border only on first joint. First joint apically on one side with 1 row of sensilla basiconica (Fig. 15B).

Mandible: with 5 rows of pectinate lamellae, number of teeth decreasing proximad (Fig. 16D). Condylus with single, strongly developed step near apical margin (Fig. 16D).

Gnathochilarium: ventral side with numerous, long bristles (Fig. 15E). Lateral of palpi 4 sensory cones, located together (Fig. 16A, C). Depression on backside of palpi with some sensory cones (Fig. 16A). Two different types of sensory uvulae on central pads: long, cylinder-shaped ones with 1 pit in their middle and more plain ones without pit (Fig. 16A, B).

Epipharynx: with numerous spines, similar in shape to all known species of giant pill-millipedes (Figs 15D).

Collum: anterior margin with 20-30 long hairs arranged in one row. Posterior margin and edges

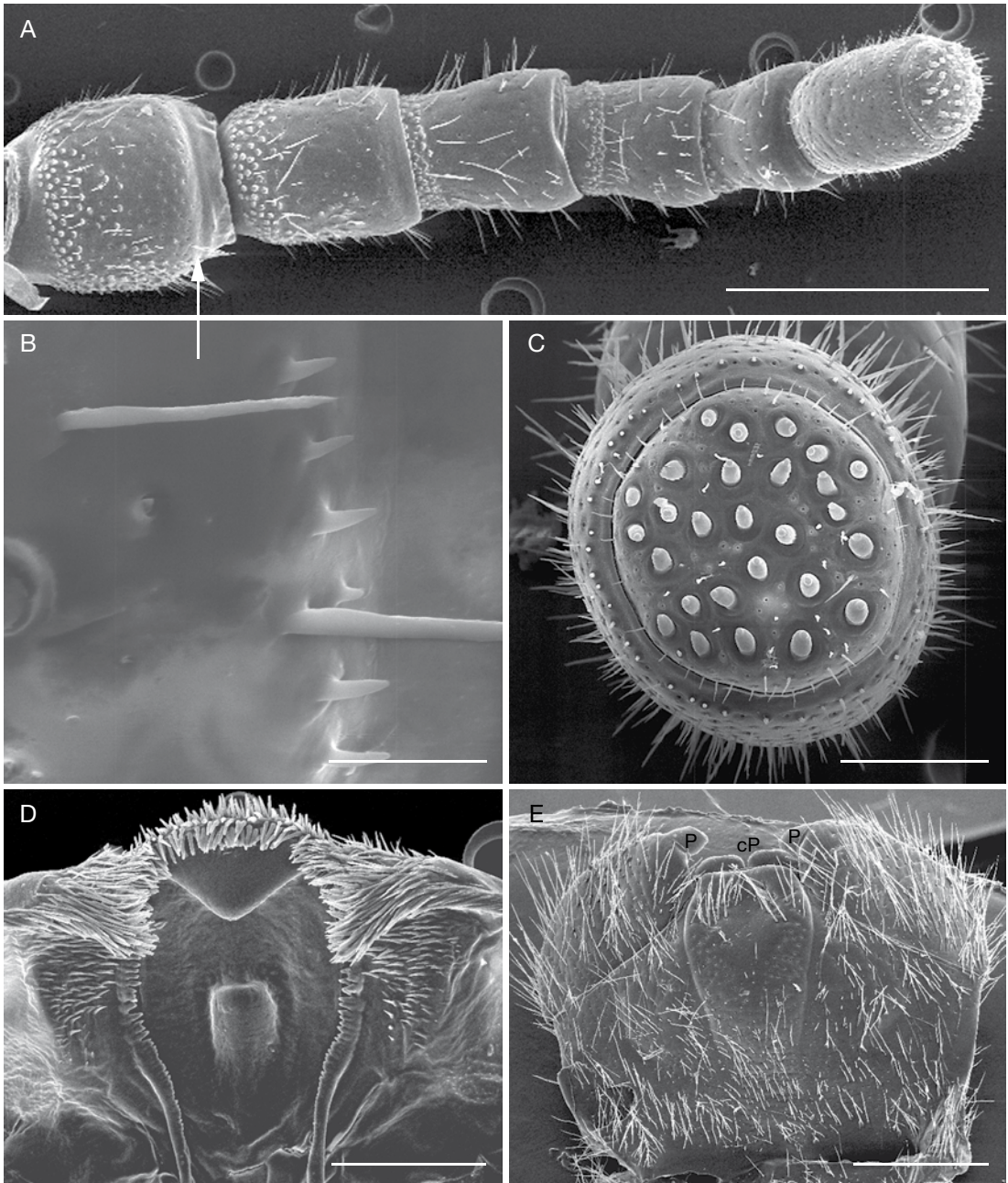


FIG. 15. — *Zoosphaerium priapus* (de Saussure & Zehntner, 1897), SEM, ♂ (FMNH 3911): **A–C** right antenna; **A**, overview; **B**, sensory (?) cones on first joint; **C**, 6th joint, apical view; **D**, epipharynx, overview; **E**, gnathochilarium, anterior side. Abbreviations: **cP**, central pads; **P**, palpus. Scale bars: A, 1 mm; B, 40 µm; C, 200 µm; D, 400 µm; E, 1 mm.

with 12-15 fine long hairs. Remaining part of column glabrous.

Thoracic shield: with few, but long hairs in the concave lateral extension of thoracic shield, especially at margins.

Tergites: tips of posterior paratergite margins slightly projecting posteriorly. Tergites smooth and glabrous.

Endotergum: internal section with short spines and few, isolated bristles (Fig. 16E). One row of small, circular cuticular patterns between marginal ridge and internal area (Fig. 16E). Externally two, in some rare cases three rows of marginal bristles, placed closely to one another. Bristles long, surmounting tergite (Fig. 16E).

Anal shield: extraordinary well-rounded, neither bell-shaped nor tapered. Reaching its hindmost point slightly above its lower side. In contrast to glabrous and smooth tergites with rough, leather-like surface, particularly towards hindmost end. In male specimens covered with numerous small hairs. Underside carries 2 black locking carinae on both sides, anterior one small, but well-developed, posterior carina dot-like, in some specimens even completely absent (Fig. 14C). Locking carinae separated from each other by a distance equal to twice the length of shorter carina (Fig. 14C).

Legs: first tarsi with 2 or 3, second with 2-4 long ventral spines. Third tarsi with 3 or 4 long and two short ventral spines. First 3 (!) tarsi with only weakly curved claws and without apical spine. Tarsi 4-21 with curved claws, 8 or 9 ventral spines and an apical spine. Legs, especially the femur (Fig. 14B), short (femur 1.45 times longer than wide, in *Z. arborealis* is the femur twice longer than wide). Tarsi 3.2 times longer than wide (in *Z. alluaudi* 4.2, in *Z. arborealis* even 5.5 times longer than wide).

Stigma-carrying plate: first stigma-carrying plate lobe long, surmounting coxa 1, covered sparsely with hairs. Lobe almost straight and only weakly curved towards coxa (Fig. 14A).

Female sexual characters: subanal plate with a washboard, consisting of well-developed stridulation ribs, 2 up to 4 ribs on each side. Stridulation ribs symmetrical, strong and long, ending shortly before the posterior margin (Fig. 14E). Vulva large,

covering more than 4/5 of coxa (Fig. 14D). Operculum high, surmounting apical edge of coxa. Apical margin of operculum medially notched, with 2 rounded lateral tips, both tips protruding to same height (Fig. 14D). Inner plate protruding almost as high as operculum (Fig. 14D).

Male sexual characters: male gonopore small, covered with one large, sclerotized, undivided and rounded plate. Plate covered with few, isolated, long hairs. Apical part of plate membranous. Gonopore covering 1/3 of height and 3/5 of width of coxa (Fig. 14F). Anal shield well-rounded, covered with field of small hairs around its hindmost point.

Anterior telopods: first joint with a stridulation harp and 2 stridulation ribs. Both ribs straight and of same length (Fig. 14G). Second joint on posterior side with lobe-like, weakly curved process with rounded edges (Fig. 14I, J). Point of process with sclerotized spots, reaching almost as high as third joint (Fig. 14I). Third joint with a cavity juxtaposed to second joint process. Apical margin of third joint well-rounded, laterally with a projection. Inner margin and lateral projection arched towards second joint. Internal margin towards cavity with numerous sclerotized spots and 4 small spines, three of them located closely towards tip (Fig. 14H). One additional short spine standing inside of cavity juxtaposed to second joint (Fig. 14G-J).

Posterior telopods: third joint weakly curved. Hollowed-out margin towards second joint with two non-sclerotized lobes and up to four smaller, sclerotized spines (Fig. 14K). In posterior view a row of *c.* 18 crenulated teeth (Fig. 14L). Immobile process as broad as third joint, with weakly curved tip. Anterior side basally with 1 membranous lobe, and 1 short sclerotized spine, furthermore whole inner margin covered with numerous small sclerotized spots juxtaposed to third joint. Third joint only basally with few isolated hairs, on rest of surface hairs absent. First and second joint on both sides with some isolated hairs (Fig. 14K, L).

INTRASPECIFIC VARIATION

Too few male specimens were among the material examined to evaluate if the males in this species are significantly smaller than females or not. Generally,

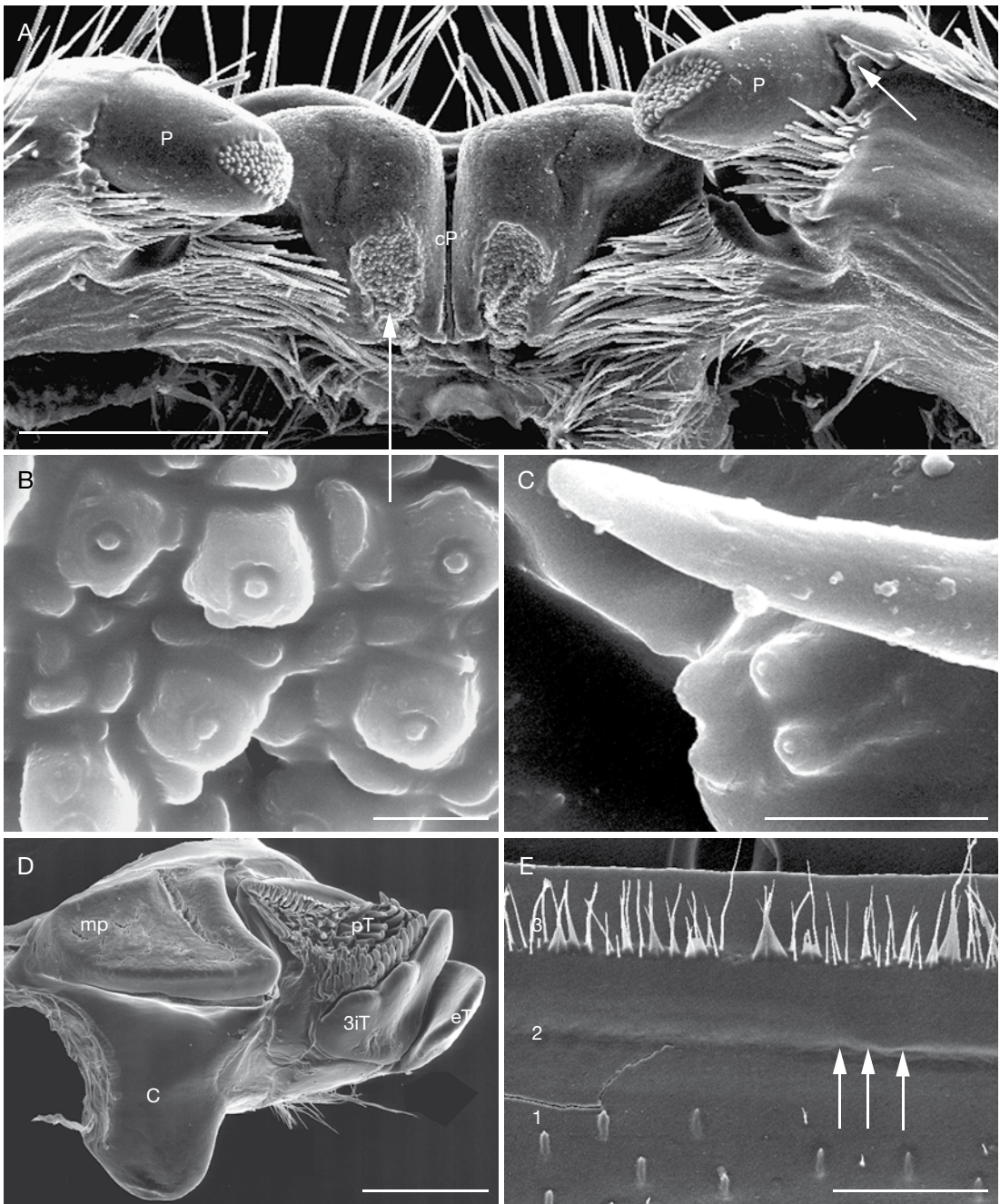


FIG. 16. — *Zoosphaerium priapus* (de Saussure & Zehntner, 1897), SEM, ♂ (FMNH3911): **A–C** gnathochilarium; **A**, apical view; **B**, sensory cones on central pads; **C**, sensory cones lateral of left palpus; **D**, right mandible; **E**, endotergum of midbody tergite, overview, arrows mark row of small, circular cuticular impressions. Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section; **3iT**, 3 internal teeth; **C**, condylus; **cP**, central pads; **eT**, external tooth; **mp**, molar plate; **P**, palpus; **pT**, pectinate lamella. Scale bars: A, 400 μ m; B, 6 μ m; C, 20 μ m; D, 600 μ m; E, 300 μ m.

smaller individuals have better-developed second locking carinae on the anal shield and seem to have a fewer number of antennal cones on antennae (15–20 in specimens < 20 mm, 21–25 in specimens > 22 mm). Furthermore, small females have a fewer number of stridulation ribs on the washboard. The number of tarsal spines and the shape of the anal shield are constant in all specimens.

DISTRIBUTION AND ECOLOGY

This species was until now only known from its first description with the locality “Antananarivo”. It remains unclear if the specimens were really collected in or around the capital of Madagascar or if they were just purchased there by Catat. The only reliable locality of this conspicuous coloured species is the littoral forest of Orangea in the far north part of the island (Fig. 13). It is unclear if this species is endemic to this single forest or to the littoral forest ecosystem. The brown-blackish coloration pattern, the long hairs on the legs and particularly the short, broad legs suggest that *Z. priapus* lives inside the soil. No other giant pill-millipede species was collected in Orangea forest.

CONSERVATION

Because the species is until now only known from the littoral forest in Orangea, its prospects of survival are directly connected with the survival of this forest. Because of the fast ongoing destruction, especially of the littoral forest ecosystem (de Gouvenain & Srilander 2003), *Z. priapus* is possibly in an urgent threat of extinction.

Zoosphaerium anomalum

(de Saussure & Zehntner, 1902)

(Figs 17; 18)

Sphaerotherium anomalum de Saussure & Zehntner, 1902: 56, pl. 15, figs 7–7e.

Zoosphaerium anomalum – Jeekel 1999: 13 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — 1901, leg. C. Alluaud, ♂ holotype (MNHN CB009).

TYPE LOCALITY. — Madagascar, Isaka XII. Remark: locality probably: province Toliara, Isaka, 24°28'S, 46°36'E.

DIAGNOSIS. — Holotype 20 mm long. Colour in alcohol jade-like green (Fig. 6A). Surface of tergites shiny, smooth and glabrous. Apical joint of antenna with 4 sensory cones. Third joint of posterior telopods weakly curved, posterior side with up to 25 sclerotized teeth, 2 large, non-sclerotized lobes and around 2 sclerotized spines (Fig. 17I, J). Second joint with broad and stout process, curved with its tip towards third joint. Second and third joints on both sides covered completely with numerous small pits, one short hair standing in each. Two basally fused stridulation ribs on male harp. Anal shield with 2 locking carinae, first short, second twice longer than first (Fig. 17C). Female unknown.

SIMILAR SPECIES

The numerous pits and hairs on the posterior telopods and the unusual shape of anterior telopods allow a secure separation from all other described Malagasy sphaerotheriids.

DESCRIPTION

Body measurements (male holotype): length 20.25, width of thoracic shield 10.5, height of thoracic shield 6.1.

Habitus: body short and massive (Fig. 17A). Tergites polished and glabrous. Anal shield only weakly rounded, with relatively steep slope (Fig. 17A).

Coloration: tergites jade-like (Fig. 19A). Head, collum, antennae and legs green.

Head: posterior margin of head towards collum without patch of small hairs.

Antennae: sixth joint longest, of cylindrical shape, with four sensory cones. First joint remarkably broader than the others, but short and without groove. Mouthparts not dissected.

Collum: only at margins with some single, long, isolated hairs, remaining parts of collum glabrous.

Thoracic shield: with few hairs in concave lateral extension (Fig. 17A).

Tergites: tips of posterior paratergites margin of almost straight, only slightly projecting posteriorly (Fig. 17A). Tergites shiny and glabrous.

Endotergum: internal section with short spines and few, isolated bristles. One row of weak, elliptical

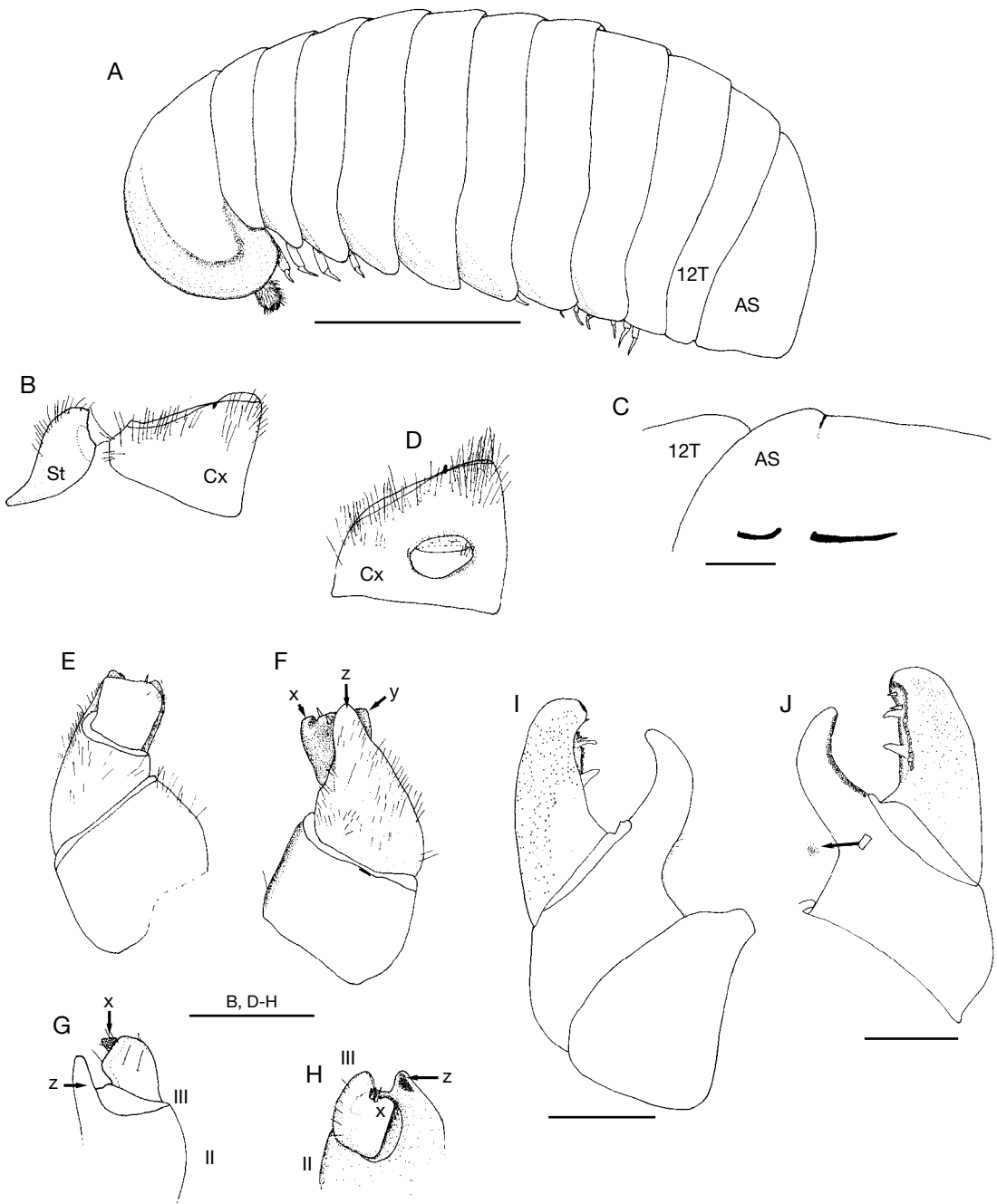


FIG. 17. — *Zoosphaerium anomalum* (de Saussure & Zehntner, 1902), holotype: **A**, habitus, body length 20.2 mm; **B**, coxa of 1st right leg with 1st stigma-carrying plate, posterior view; **C**, closing ledges of anal shield; **D**, coxa of 2nd right leg with gonopore; **E-H**, left anterior telopod; **E**, anterior view; **F**, posterior view; **G**, lateral view; **H**, inner view; **I, J** left posterior telopod; **I**, anterior view; **J**, posterior view. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **St**, stigma-carrying plate; **x**, inner process of joint 3 of anterior telopods; **y**, lateral process of joint 3 of anterior telopods; **z**, process of joint 2 of anterior telopods. Scale bars: **A**, 5 mm; **B-J**, 1 mm.



FIG. 18. — *Zoosphaerium anomalum* (de Saussure & Zehntner, 1902), holotype, SEM endotergum: **A**, overview; **B**, marginal bristle, detail. Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section. Scale bars: A, 200 μ m; B, 20 μ m.

grooves between marginal ridge and internal area (Fig. 18A). Externally one row of marginal bristles, standing apart from one another. Bristles scaly (Fig. 18B), short, protruding 1/2-2/3 between basal point of bristles and tergite margin (Fig. 18A).

Anal shield: only weakly rounded, with an almost steep slope. Reaching its hindmost point on a small process at its lower side (Fig. 17A). In contrast to polished and smooth tergites with numerous small pits, all supporting a short hair. Pits located only on slope, especially towards its hindmost point. Underside carrying 2 black locking carinae on both sides, anterior one small, but well-developed, posterior carina twice longer than first (Fig. 17C). Locking carinae separated from one another by a distance equal to 1/2 of shorter carina length (Fig. 17C).

Legs: first tarsi with 5 or 6, second with 6 long ventral spines. First 2 tarsi with only weakly curved claws and without apical spine. Tarsi 3-21 with curved claws, 6 or 7 ventral spines and an apical spine. Femora with crenulated ridge.

Stigma-carrying plate: first stigma-carrying plate lobe long, surmounting coxa 1, covered sparsely with hair around its apical margin. Lobe almost straight and only weakly curved towards coxa, with pointed tip (Fig. 17B).

Female unknown.

Male sexual characters: male gonopore small, covered with single, large, sclerotized, undivided and rounded plate. Apical part of plate membranous. Gonopore covering 1/3 of coxal height and 2/5 of its width (Fig. 17G). Anal shield almost rectangular, with steep slope, covered with field of small (sensory?) hairs standing in small pits, particularly around hindmost point.

Anterior telopods: syncoxite destroyed. First joint with a stridulation harp and 2 stridulation ribs. Ribs starting basally as one rib, at half of length they diverge into 2 ribs. Both ribs straight and of same length. Second joint on posterior side with lobe like, weakly curved process with rounded edges (Fig. 17G, H). Point of process protruding as high as third joint. Process towards third joint with sclerotized spots (Fig. 17H). Third joint with



FIG. 19. — **A**, *Zoosphaerium anomalum*, holotype; **B**, *Z. piligerum*, small female (BLF 2543). Scale bars: A, 10 mm; B, 2 mm.

a deep cavity juxtaposed to second joint. Internal part with a long process, protruding posteriorly. Tip of process on its inner side completely covered with small, sclerotized spots (Fig. 17G). Apical margin of third joint with 3 short, sclerotized spines (Fig. 17F). First joint only on borders with few, isolated hairs.

Posterior telopods: third joint weakly and irregularly curved. Hollowed-out margin towards second joint with two non-sclerotized lobes and two smaller, sclerotized spines (Fig. 17I), on posterior aspect with one row of *c.* 25 crenulated teeth (Fig. 17J). Process of second joint slightly more slender than third joint, with curved tip. On posterior side whole inner margin covered with numerous small, sclerotized spots juxtaposed to third joint. Second and third joint without any long hair, but on both sides almost completely covered with small pits, each support a small sensory (?) hair (Fig. 17I, J).

DISTRIBUTION AND ECOLOGY

This species is only known from its first description, giving the locality “Isaka”. Isaka is a rainforest located in the Andohahela area (Fig. 13).

CONSERVATION

Because the species is until now only known from one single locality in pristine rainforest (Fig. 13), and it was furthermore not found in recently collected

material, it is possible that *Z. anomalum* is in urgent threat of extinction.

Zoosphaerium coquerelianum species-group

SPECIES INCLUDED. — *Zoosphaerium coquerelianum* (de Saussure & Zehntner, 1897); *Z. alluaudi* (de Saussure & Zehntner, 1897); *Z. voeltzkowianum* (de Saussure & Zehntner, 1897); *Z. villosus* Wesener & Sierwald, 2005.

DIAGNOSIS. — These Malagasy giant pill-millipede species share a number of derived characters, identifying them as a species-group. Species of this group can be identified by a striking similarity in the shape of posterior telopods (Figs 20J; 24K). The third joint of the posterior telopods is broadened, 2–2.5 times longer than wide. The hollowed-out margin of the third joint and especially the row of sclerotized teeth reaches from the tip down to only half of the joints length (Figs 20K; 24L). The locking carinae of the anal shield are similar in all species, the posterior carina being 2.5–4 times longer than the anterior carina (Figs 20B; 24D). Inside the species-group the species are clearly distinguishable by numerous characters like the shape of the anterior pair of telopods, the number of sensory cones on the antenna, sensory cones on gnathochilarium, the shape of the female operculum, body size, bristle patterns on collum and different structures on the tergite surface (see also Wesener & Sierwald 2005a). A phylogenetic analysis will be necessary to confirm if the *coquerelianum*-group represents a monophyletic group among Malagasy sphaerotheriids, which then may deserve genus status.

KEY TO THE *ZOOSPHAERIUM COQUERELIANUM* SPECIES-GROUP

1. Antenna with more than 10 sensory cones 2
— Antenna with 4 sensory cones (Fig. 27A) 3
2. Anterior telopods with 1 stridulation rib (Fig. 20F) *Z. coquerelianum*
— Anterior telopods with 2 stridulation ribs *Z. villosum*
3. Anal shield surface covered with short hair. Posterior locking carina of anal shield 2.5-3 times longer than anterior carina *Z. alluaudi*
— Anal shield surface glabrous. Posterior locking carina of anal shield more than 3.5 times longer than anterior carina *Z. voeltzkowianum*

Zoosphaerium coquerelianum (de Saussure & Zehntner, 1897) (Figs 20-22)

Sphaerotherium coquerelianum de Saussure & Zehntner, 1897: pl. 1, figs 1c, 2a-c, pl. 5, fig. 11; 1902: 42, pl. 15, fig. 1.

Heligmasoma errans Chamberlin, 1921: 58, n. syn.

Zoosphaerium amittum Chamberlin, 1921: 59, n. syn.

Zoosphaerium coquerelianum – Jeekel 1999: 11 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — *Zoosphaerium coquerelianum*: VI.1862, leg. Coquerel, ♂ lectotype (broken, here designated), (MNHN CB015); 2 ♀♀ paralectotypes (MNHN CB015); Madagascar, 1862, leg. Coquerel, no. 6, 1 ♀ paralectotype (MNHN CB018).

Heligmasoma errans: ♂ holotype, no collection data (MCZ 4692); 1 ♂, 2 ♀♀ paratypes (MCZ 4693).

Zoosphaerium amittum: ♀ holotype (MCZ 4709).

TYPE LOCALITY. — *Zoosphaerium coquerelianum*: Madagascar.

Heligmasoma errans: unknown.

Zoosphaerium amittum: uncertain, but probably Madagascar (“Whyman coll.”).

OTHER MATERIAL EXAMINED. — **Madagascar**. Leg. Grandidier, 2 ♂♂, 1 ♀ (MNHN CB017).

DIAGNOSIS. — Up to 63 mm long. Colour brown, posterior margin of tergites dark brownish, some smaller specimens with olive-greenish spots. Surface of tergites structured similar to an orange surface, glabrous. Anal shield well-rounded, glabrous. Apical antennomere with 18-29 sensory cones. Third joint of posterior telopods broad, with well-rounded tip. Posterior side with up to 7 sclerotized black teeth, 1 small non-sclerotized lobe and 3 sclerotized spines (Fig. 20J, K). Second joint with long and slim, curved process, basally with 1 large

spine. One stridulation rib on male harp (Fig. 20F) and 2 or 3 on each side of female washboard. Anal shield with 2 locking carinae, first small, second more than 2.5 times longer than first (Fig. 20B). Operculum of vulva small, not protruding above coxa, apically with 2 well-rounded lobes protruding to same height. Interior plate of vulva protruding as high as operculum (Fig. 21A, B).

SIMILAR SPECIES

All species of the *coquerelianum*-group show similarly shaped telopods and opercula. *Zoosphaerium coquerelianum* is the only described species in this group that possess a single stridulation rib on the male harp. This feature identifies the large species unambiguously.

DESCRIPTION

Body measurements: males (3 specimens): length up to 22.00 (largest broken), width of thoracic shield up to 18.55, height of thoracic shield up to 10.55. Females (5 specimens): length up to 62.45, width up to 32.4, height up to 16.6.

Habitus: body massive and high (Fig. 20A). Tergites and anal shield without hair, but surface completely covered with irregular small pits, comparable to an orange surface.

Coloration: faded in alcohol. Tergites brown, posterior margin with thin dark brown line. Some specimens with olive green spots, resembling possibly the remains of original coloration. Head, antennae and tips of legs dark green.

Head: posterior margin of head towards collum without small hair.

Antennae: long, sixth joint of cylindrical shape with 18-29 sensory cones. First joint remarkably

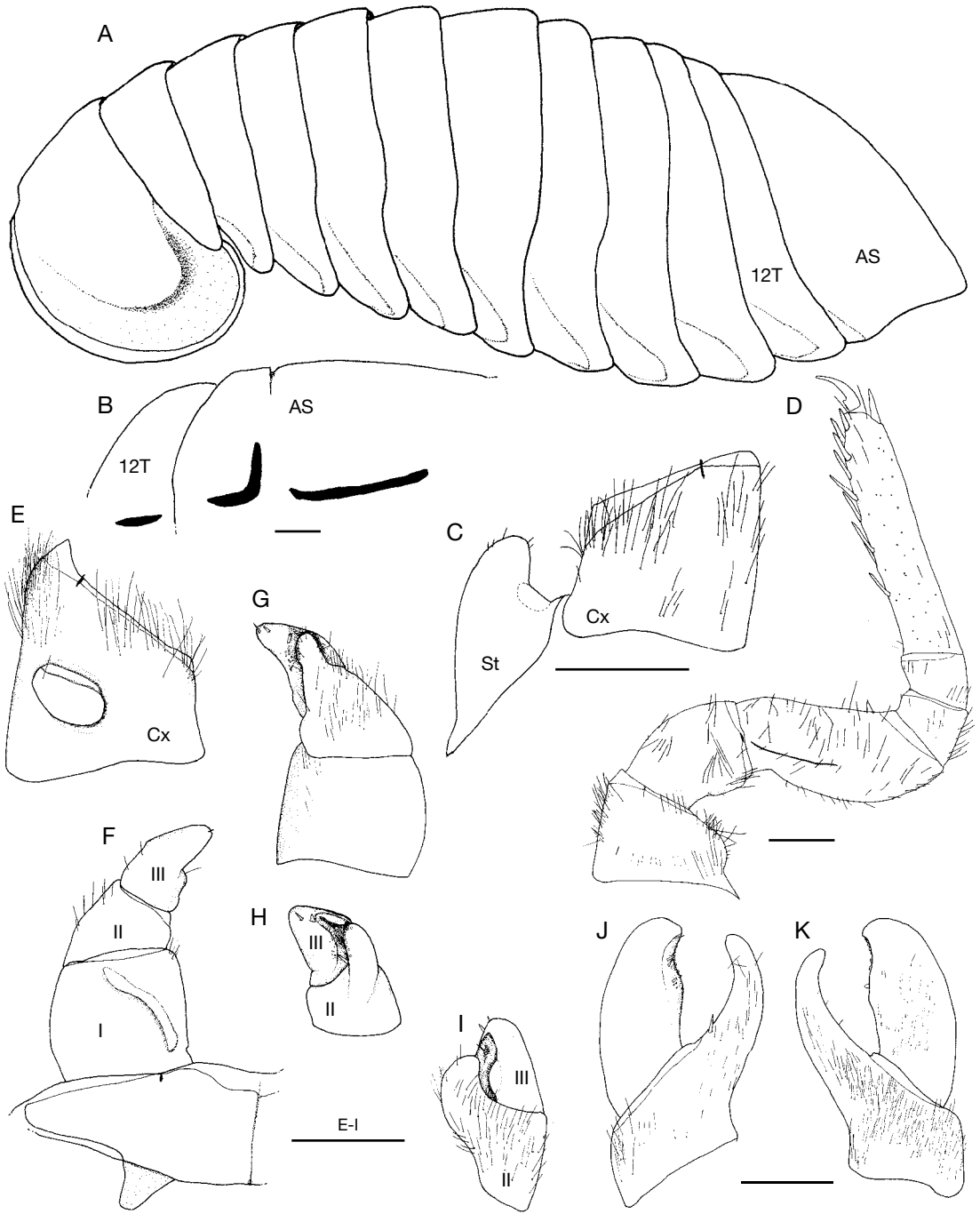


FIG. 20. — *Zoosphaerium coquerelianum* (de Saussure & Zehntner, 1897), lectotype: **A**, habitus, body length 22 mm; **B**, closing ledges of anal shield; **C**, coxa of 1st right leg with 1st stigma-carrying plate; **D**, 9th left leg; **E**, coxa of 2nd left leg with gonopore; **F-I** left anterior telopod; **F**, anterior view; **G**, posterior view; **H**, inner view; **I**, lateral view; **J, K**, left posterior telopod joints 2 and 3; **J**, anterior view; **K**, posterior view. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **St**, Stigma-carrying plate. Scale bars: B-K, 1 mm.

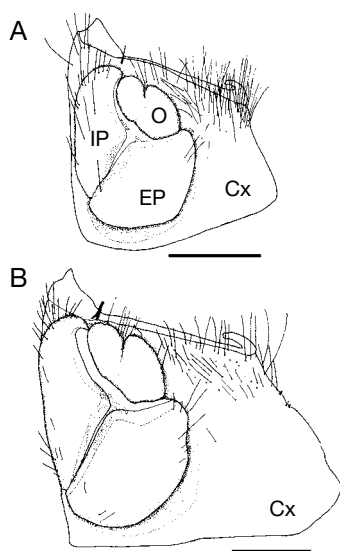


FIG. 21. — *Zoosphaerium coquerelianum* (de Saussure & Zehntner, 1897), coxa of 2nd left leg with vulva (paralectotypes): **A**, small female (MNHN CB015); **B**, large female (MNHN CB018). Abbreviations: **Cx**, coxa; **EP**, exterior plate; **IP**, inner plate; **O**, operculum. Scale bars: 1 mm.

broadly than others. At least first joint with sclerotized teeth. Mouthparts not dissected.

Collum: anterior and posterior margin with some long hairs arranged in one row. Remaining part of collum with some long, isolated hairs.

Thoracic shield: thoracic shield surface structured like those of tergites (Fig. 20A).

Tergites: anterior paratergite depressions of tergites 3-12 with isolated hairs. Tips of paratergites margins projecting posteriorly.

Endotergum: internal section with short spines and isolated bristles. One row of large circular cuticular patterns located between marginal ridge and internal area. Marginal brim strong and straight (Fig. 22A, B). Externally 2 rows of marginal bristles, standing closely to one another. Bristles scaly (Fig. 22C, D), protruding up to 1/2 towards area between basal point of bristles and tergite margin (Fig. 22E).

Anal shield: well-rounded, neither bell-shaped nor tapered (Fig. 20A). Like tergites completely covered with numerous small irregular pits, surface orange-like. Underside carrying two well-developed black

locking carinae on both sides, anterior one small, but well-developed, projecting posteriorly strongly towards anal shield margin. Posterior carina more than 2.5 times longer than first, straight (Fig. 20B). Locking carinae separated by a distance equal to half of shorter carina length (Fig. 20B).

Legs: first tarsi with 5 or 6, second with 6-8 long ventral spines. Third tarsi with 7-9 long ventral spines. First two tarsi with only weakly curved claws and without apical spine. Tarsi of legs 3-21 with curved claws, 8 or 9 ventral spines and an apical spine. Ventral spines of legs dispersed through whole inner side of tarsus. In 9th leg femur 1.9 times longer than wide, tarsi 4.9 times longer than wide. Femora with crenulated ridge of medium length (Fig. 20D).

Stigma-carrying plate: first stigma-carrying plate lobe short and well-rounded, protruding up to apical edge of coxa 1. Lobe curved towards coxa, its broad, well-rounded tip thinner than basal part (Fig. 20C).

Female sexual characters: second leg pair on lateral side with some small, black triangular spines (Fig. 21A, B). Subanal plate with a washboard, consisting of well-developed stridulation ribs, 2 up to 3 ribs on each side. Stridulation ribs symmetrical, sometimes non-continuous, especially the inner rib. Ribs long, ending just before posterior margin. Vulva large, covering slightly more than 1/2 of coxa. Operculum low, not surmounting coxa. Apical margin of operculum medially notched, with two rounded lateral tips, both of same height (Fig. 21A, B). Inner plate long and broad, protruding as high as operculum (Fig. 21A, B).

Male sexual characters: male gonopore covered with single, large, sclerotized, undivided and rounded plate. Apical part of plate membranous. Gonopore covering 1/3 of height and a little less than 1/2 of coxal width (Fig. 20D). Anal shield similar to those of females.

Anterior telopods: first joint with a stridulation harp and one stridulation rib. Rib straight, broad and well-developed (Fig. 20F). Second joint on posterior side with lobe-like, weakly curved process with rounded edges (Fig. 20G-I). Point of process protruding almost as high as third joint, towards third joint apically with sclerotized spots and basally with single spine (Fig. 20H). Third joint with

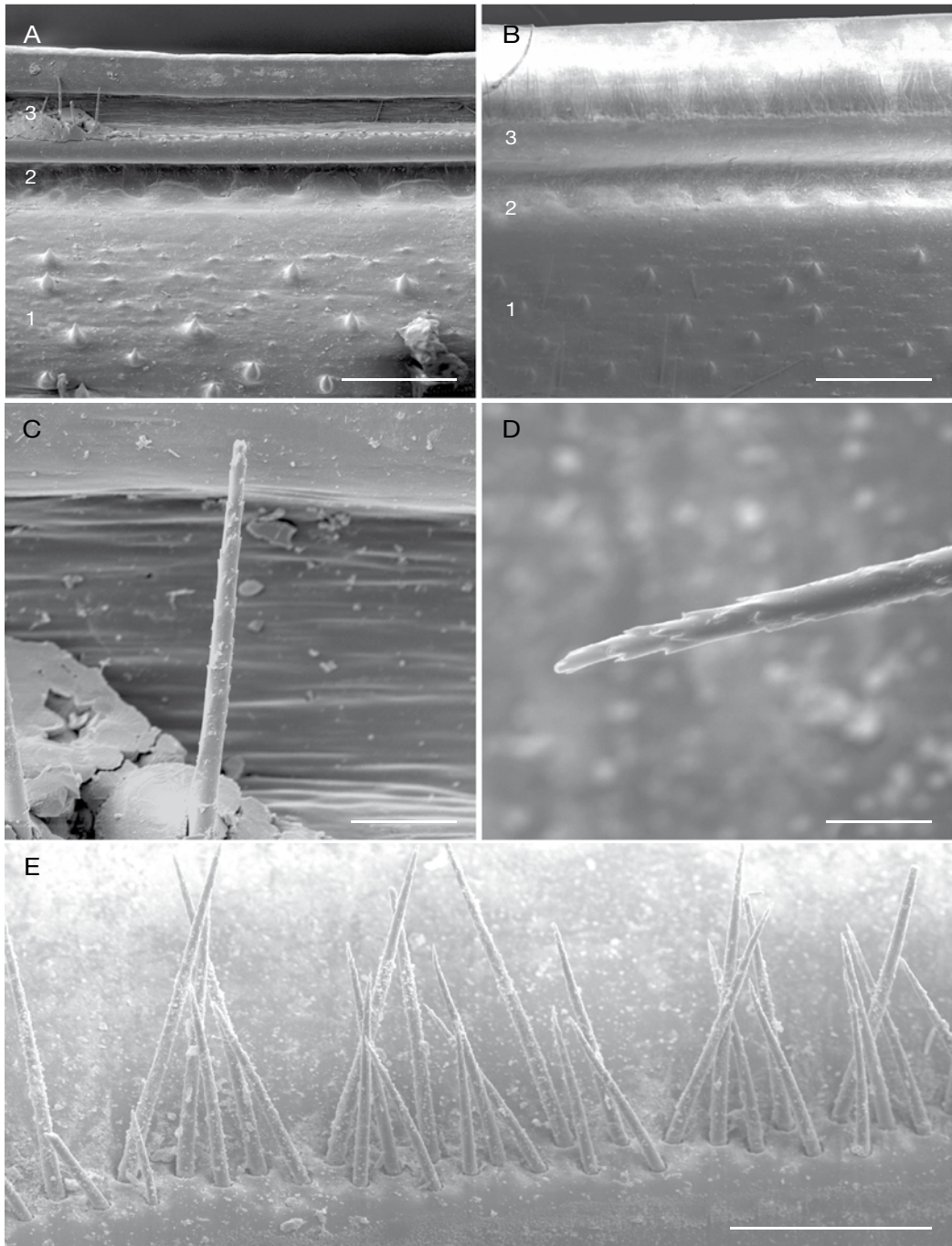


FIG. 22. — *Zoosphaerium coquerelianum* (de Saussure & Zehntner, 1897), SEM endotergum of midbody tergite: **A, C**, ♂ lectotype; **B, D, E**, ♀ paralectotype (MNHN CB018); **A, B**, overview; **C, D**, marginal bristle, detail; **E**, paralectotype area (1) detail. Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section. Scale bars: **A**, 200 μ m; **B**, 400 μ m; **C**, 20 μ m; **D**, 10 μ m; **E**, 100 μ m.

strong tip bending inwards, protruding twice as high as second joint process. Joint with a cavity juxtaposed to second joint process. Apical margin of third joint well-rounded, at internal margin towards cavity with numerous sclerotized spots and two small spines, a third spine located closely towards tip (Fig. 20G-I).

Posterior telopods: third joint weakly curved, becoming only slightly slimmer towards tip. Hollowed-out margin towards second joint with 1 small non-sclerotized lobe and up to 3 smaller, sclerotized spines, one of them located apically, the two other ones at half of its length (Fig. 20J). Third joint on posterior aspect with 1 row of *c.* 7 sclerotized black teeth (Fig. 20K). Process of second joint slim, almost as long as third joint, with a weakly curved tip. Anterior side basally with 1 sclerotized spine. Third joint on posterior side with few isolated hairs, on rest of surface hairs absent. First and second joints on both sides, particularly on posterior side, with numerous hairs (Fig. 20J, K). Inner horns of syncoxite apically curved posteriorly. Tips sharp, whole horns covered with numerous small hairs.

INTRASPECIFIC VARIATION

The material contains too few specimens to evaluate the intraspecific variation. The vulvae of small and gigantic specimens feature the same pattern (Fig. 21A, B), different to the drawing given in the first description (de Saussure & Zehntner 1897).

DISTRIBUTION AND ECOLOGY

No precise locality data exist for this species. No material was found in more recently collected material. This species is only known from the type series.

CONSERVATION

It is unusual that no material of such a large species as *Z. coquerelianum* was found in the Museum collections. It could be suggested that this species is extinct.

REMARKS

All type specimens of *Heligmasoma errans* are similar to the types of *Z. coquerelianum*. Chamberlin (1921) obviously did not compare *H. errans* with any described Malagasy Sphaerotheriida species when he

erected the new genus *Heligmasoma*. The same fits to *Zoosphaerium amittum* which was described by Chamberlin (1921) in the same paper. Chamberlin mentioned in the first description of both species only general characters, which seem to fit on almost all known Sphaerotheriida species. Hoffman (1980: 62) already noted to the genera described by Chamberlin that “although it seems probable that both are junior synonyms of some common and well-known genus”. However, if the *coquerelianum* species-group will later be elevated to genus rank, the genus name *Heligmasoma* would be available for this group.

Zoosphaerium villosum

Wesener & Sierwald, 2005

Zoosphaerium villosum Wesener & Sierwald, 2005a: 19, figs 9-16.

NEW MATERIAL. — Madagascar, forêt [illegible] native de Tsianovoha, coll. Mission R. Heim, 12-16.IX.1934, 2 ♂♂, 1 ♀ (MNHN n° 32a).

REMARK

See Wesener & Sierwald (2005b) for a complete description of this species.

For distribution, see Figure 23.

Zoosphaerium alluaudi

(de Saussure & Zehntner, 1897)

REMARK

See Wesener & Sierwald (2005a) for a redescription of this species.

For distribution, see Figure 23.

Zoosphaerium voeltzkowianum

(de Saussure & Zehntner, 1897)

(Figs 24-29)

Sphaerotherium voeltzkowianum de Saussure & Zehntner, 1897: pl. 5, fig. 21; 1901: 435, pl. 39, figs 6, 7, pl. 40, fig. 36; 1902: 52, pl. 14, figs 8-8a, pl. 15, figs 3-3a.

Sphaerotherium imbecillum de Saussure & Zehntner, 1897: pl. 5, fig. 20, n. syn.

Sphaerotherium globulus de Saussure & Zehntner, 1902: 34, n. syn.

Zoosphaerium voeltzkowianum – Jeekel 1999: 12 (lists species name). — Enghoff 2003 (lists species name).

TYPE MATERIAL. — *Zoosphaerium voeltzkowianum*: Madagascar, leg. Musée de Genève (de Saussure & Zehntner [1902: 53] mentioned “plusieurs individus de Nosy Bé, récoltés par le docteur Voeltzkow”), ♂ lectotype (here designated) (MNHN CB046); same data as lectotype, 2 ♀♀ paralectotypes.

Zoosphaerium imbecillum: Madagascar, Nosy Bé, 2 ♂♂ syntypes (MNHN CB031).

Zoosphaerium globulus: Madagascar, Nosy Bé, 4304, leg. 1885, ♂ holotype (broken) (MNHN CB025).

OTHER MATERIAL EXAMINED. — **Madagascar**. Province Antsiranana, Nosy Bé, Parc national de Lokobe, 4.95 km 125° ESE Hellville, 13°24'56"S, 48°18'27"E, 0–200 m, rainforest, pitfall trap, coll. D. Andriamalala, C. Griswold, H. Ratsirarson & D. Silva, 15.II.2003, 1 ♂ (BLF 8000).

DIAGNOSIS. — Up to 30 mm (literature: 41 mm, de Saussure & Zehntner 1902) long. Brown, posterior margin of tergites darker brownish, some specimens with traces of former green coloration. Surface of tergites glabrous, at high magnification small dot-like impressions become visible. Anal shield well-rounded (Fig. 24A), glabrous. Apical antennomere with 4 sensory cones (Fig. 28A). Third joint of posterior telopod broad, with well-rounded tip. Posterior side with around 5 sclerotized teeth and 3 sclerotized spines (Figs 24L; 25G; 26H). Second joint with long and slim, weakly curved immovable digit, basally with 1 spine, distally at inner margin with numerous sclerotized spots (Fig. 24K). Two stridulation ribs on each male harp and 2 on each side of female washboard (Figs 24F, H; 25E; 26E). Anal shield with 2 locking carinae, first small, second more than 4.5 times longer than first (Figs 24D; 25D; 26C). Operculum of vulva minute, female possibly immature (Fig. 24E).

SIMILAR SPECIES

All species in the *coquerelianum*-group show similar shaped posterior telopods and female vulvae. *Zoosphaerium voeltzkowianum* features nevertheless a unique combination of characters, as 4 antennal sensory cones, 2 stridulation ribs on the male harp, glabrous collum, absence of sclerotized teeth on the third joint of anterior telopods and the length of the posterior locking carina.

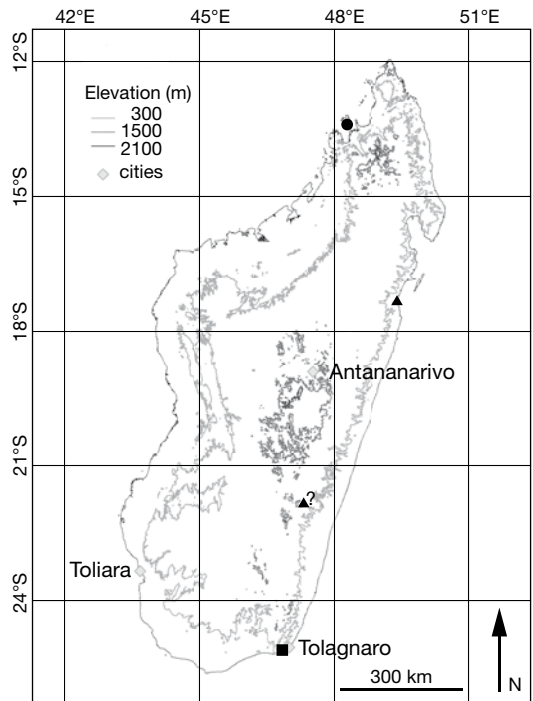


FIG. 23. — Distribution map of *Zoosphaerium alluaudi* (de Saussure & Zehntner, 1897) (■), *Z. villosum* Wesener & Sierwald, 2005 (▲) and *Z. voeltzkowianum* (de Saussure & Zehntner, 1897) (●).

DESCRIPTION

Body measurements: males (5 specimens): length up to 30.25 (largest broken), width of thoracic shield up to 15.5, height of thoracic shield up to 9.2. Females (2 specimens): length up to 27.2 (literature 41.0 mm), width up to 13.7, height up to 7.95.

Habitus: elongated, not high (Figs 24A; 25A; 26A). Tergites and anal shield without hair, but surface of tergite and anal shield at high magnification covered with small, irregular circular pits.

Coloration: faded in alcohol. Tergites brown, posterior margin with thin dark brown line. Sometimes traces of shiny green coloration visible. Head, antennae and tips of legs green.

Head: posterior margin of head towards collum without small hair.

Antennae: length of joints: 1>2>3=4=5<<6 (Fig. 28A), sixth joint longest, of cylindrical shape (Fig. 28A), apically with 1 row of sensilla basiconica, on tip bearing a disc with 4 (5) sensory cones.

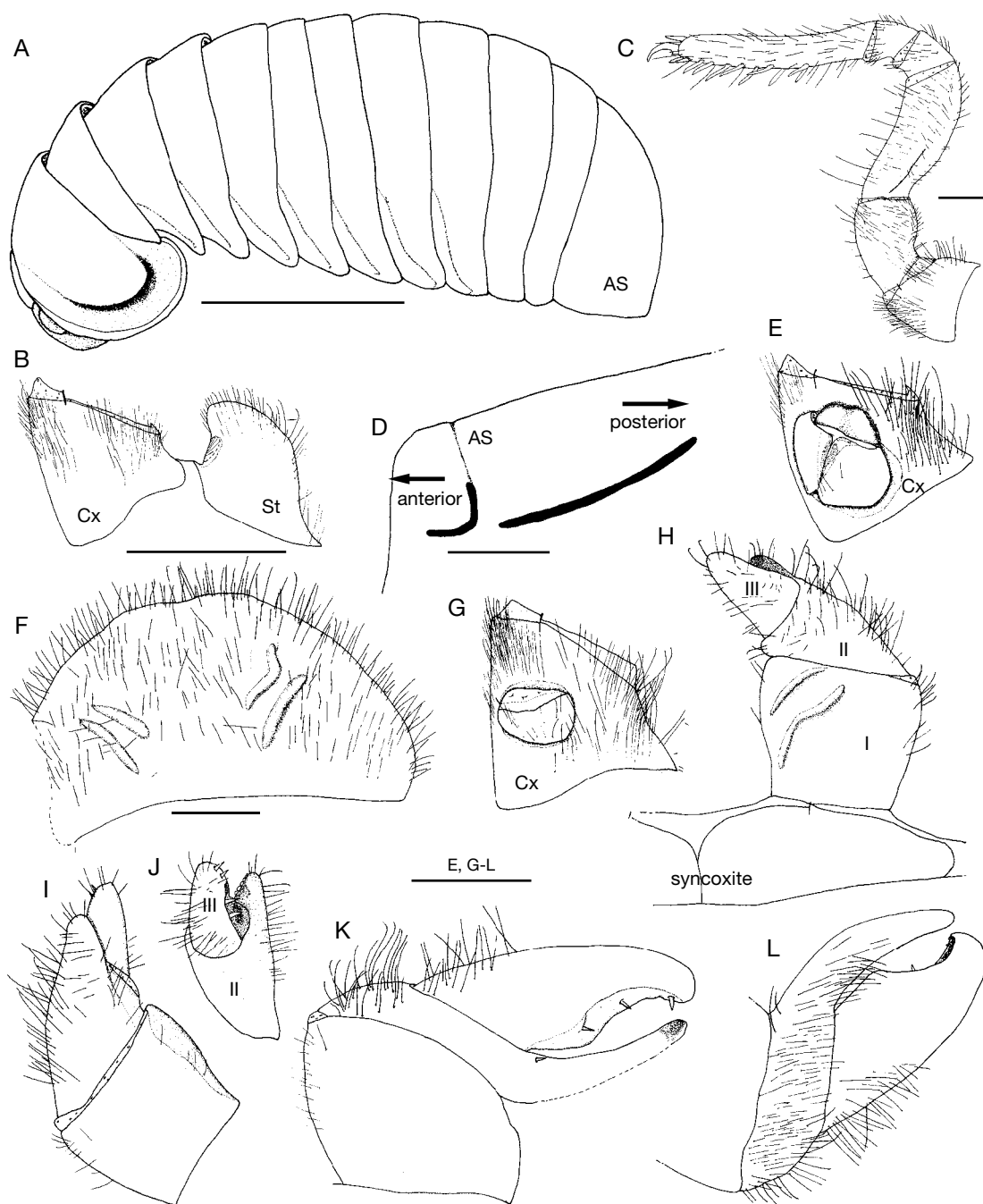


FIG. 24. — *Zoosphaerium voeltzkowianum* (de Saussure & Zehntner, 1897): **A-D, G-L**, lectotype; **E, F**, paralectotype; **A**, habitus, body length 30 mm; **B**, coxa of 1st left leg with 1st stigma-carrying plate **C**, 9th left leg; **D**, closing ledges of anal shield, left side; **E**, coxa of 2nd left leg with vulva; **F**, subanal plate; **G**, coxa of 2nd left leg with gonopore; **H-J**, right anterior telopod; **H**, anterior view; **I**, posterior view; **J**, inner view; **K, L**, left posterior telopod; **K**, anterior view; **L**, posterior view. Abbreviations: **AS**, anal shield; **Cx**, coxa; **St**, stigma-carrying plate. Scale bars: **A**, 10 mm; **B-L**, 1 mm.

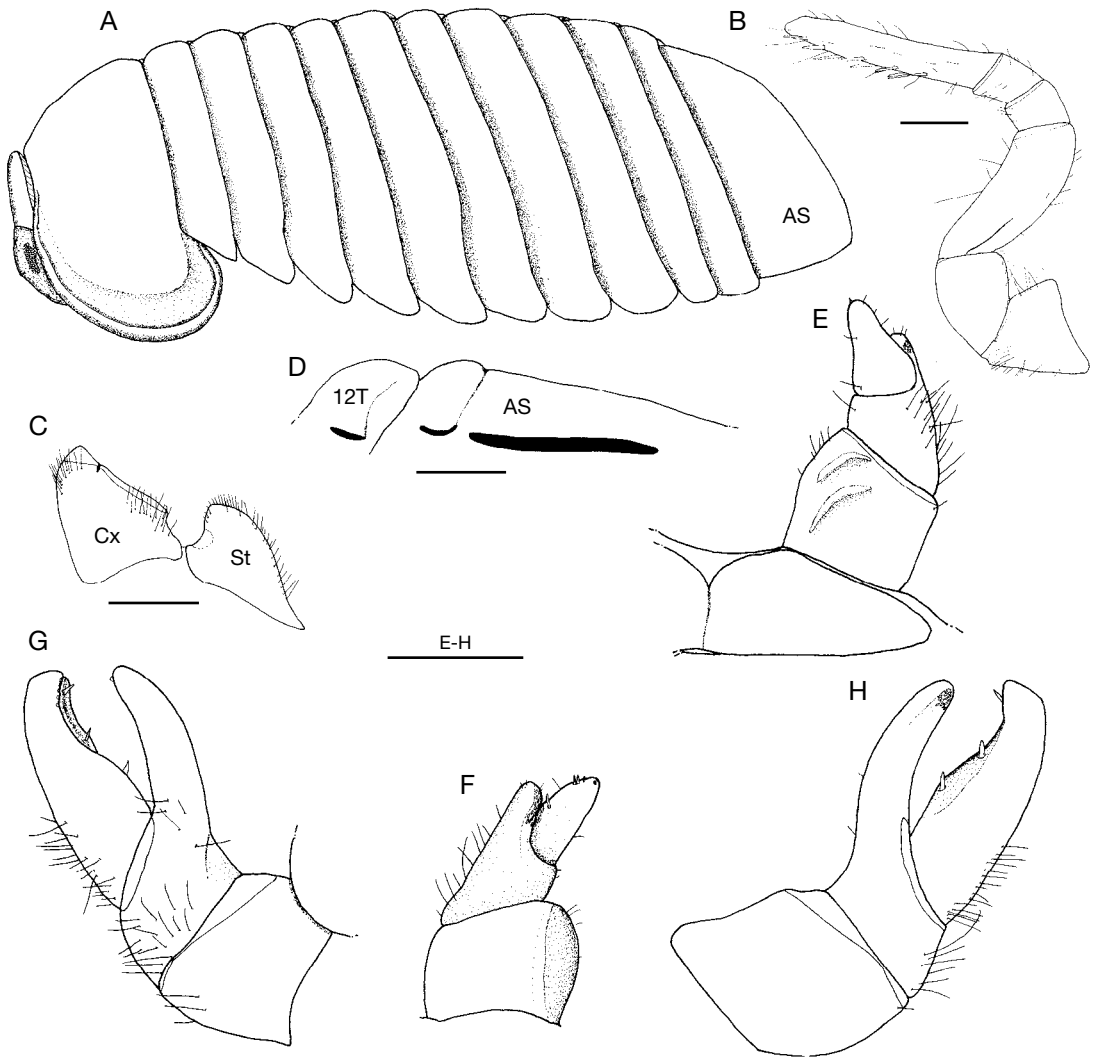


FIG. 25. — *Zoosphaerium voeltzkowianum* (de Saussure & Zehntner, 1897), paralectotype of *Z. imbecillum* n. syn.: **A**, habitus, body length 20 mm; **B**, 9th left leg; **C**, coxa of 1st left leg with 1st stigma-carrying plate; **D**, closing ledges of anal shield; **E**, **F**, right anterior telopod; **E**, anterior view; **F**, posterior view; **G**, **H**, right posterior telopod; **G**, posterior view; **H**, anterior view. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **St**, stigma-carrying plate. Scale bars: B-H, 1 mm.

(Fig. 28A). First joint remarkably broader than the others, short and with one groove (Fig. 28A). Sclerotized teeth at the base of joints 1-3, reaching not up to apical border. First joint apically on one side with 1 or 2 rows of sensilla basiconica (Fig. 28B).

Mandible: with 6 rows of pectinate lamellae; number of teeth decreasing proximad (Fig. 27A).

Condylus with 2 strongly developed steps near apical margin, apical step stronger developed (Fig. 27A).

Gnathochilarium: ventral side with numerous bristles (Fig. 27B). Bump with 4 sensory cones, located together lateral of palpi (Fig. 27D). Vale on backside of palpi with numerous sensory cones (Fig. 28C). Two different types of sensory uvulae on

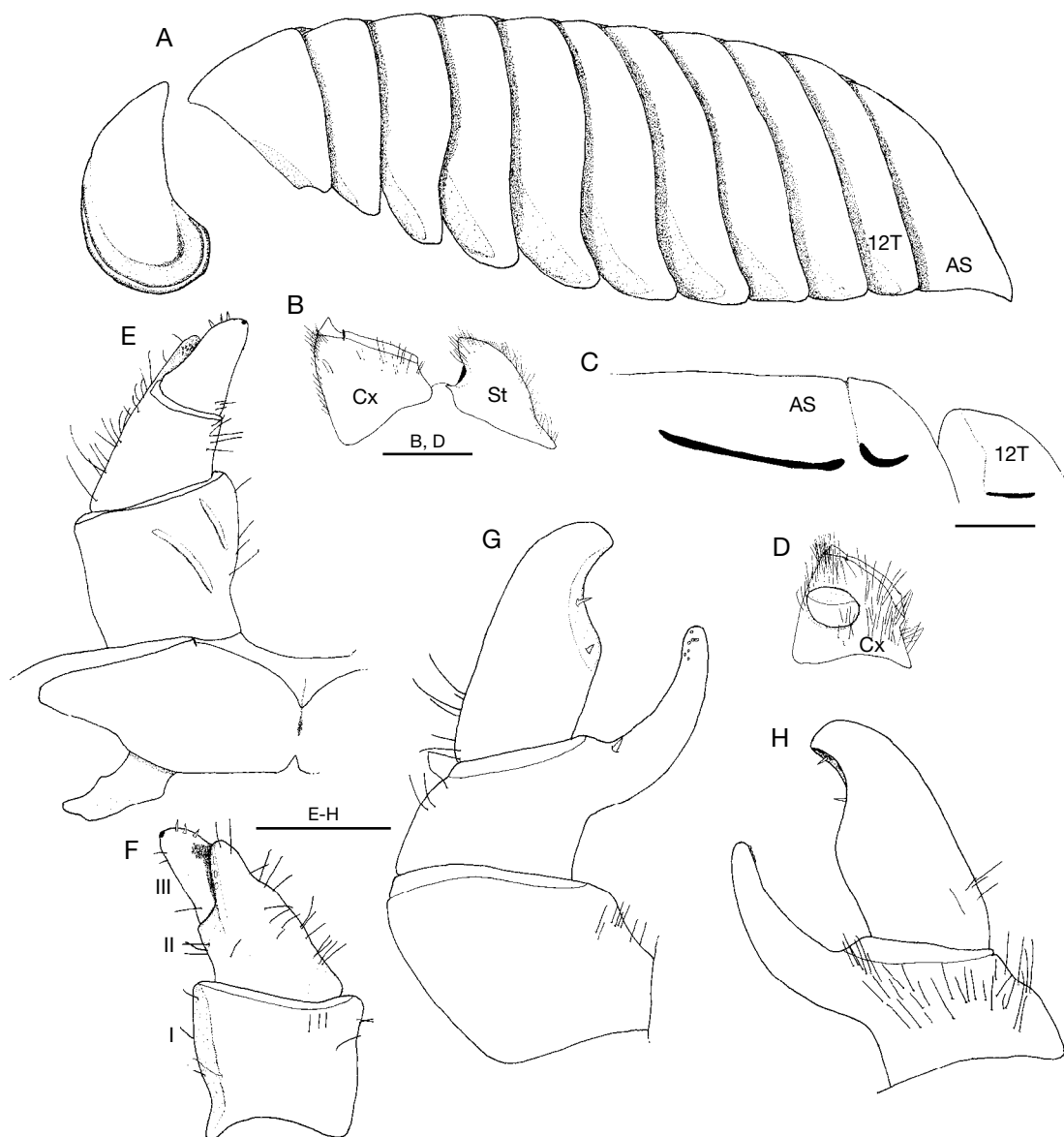


FIG. 26. — *Zoosphaerium voeltzkowianum* (de Saussure & Zehntner, 1897), holotype of *Z. globulus* n. syn.: **A**, habitus, body length 28 mm; **B**, coxa of 1st left leg with 1st stigma-carrying plate; **C**, closing ledges of anal shield; **D**, coxa of 2nd left leg with gonopore; **E**, **F**, left anterior telopod; **E**, anterior view; **F**, posterior view; **G**, **H**, left posterior telopod; **G**, anterior view; **H**, posterior view. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **St**, stigma-carrying plate. Scale bars: B-H, 1 mm.

central pads: long, cylinder-shaped ones with single pit in their middle and more plain ones without pit (Figs 27C; 28C).

Collum: anterior and posterior margin with some long hairs arranged in one row. Remaining part of collum glabrous.

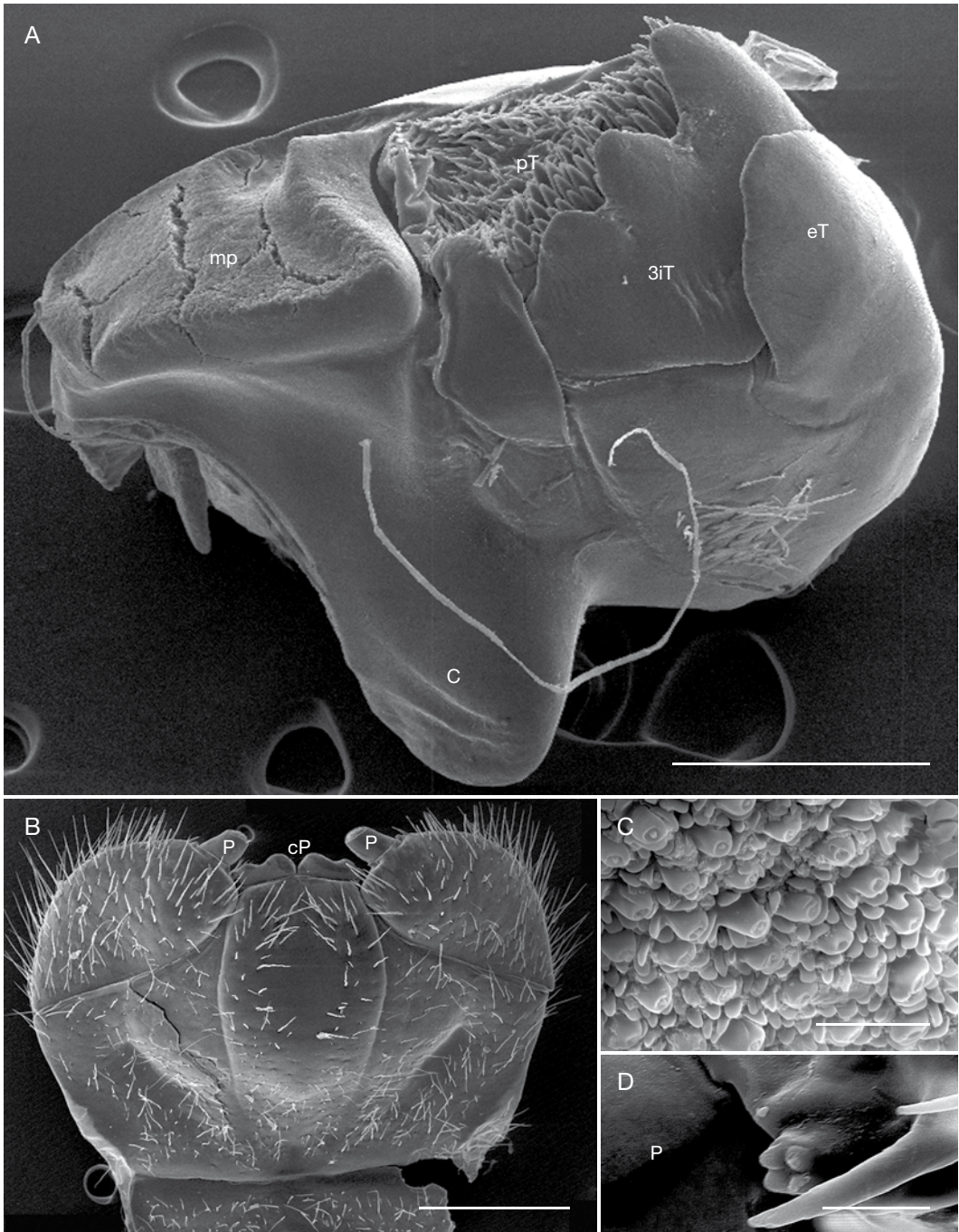


FIG. 27. — *Zoosphaerium voeltzkowianum* (de Saussure & Zehntner, 1897), SEM (BLF 8000): **A**, right mandible, overview; **B**, gnathochilarium, anterior side; **C**, sensory cells on central pads of gnathochilarium; **D**, sensory cones lateral of left gnathochilarium palpus. Abbreviations: **3iT**, 3 internal teeth; **C**, condylus; **cP**, central located pads; **eT**, external tooth; **mp**, molar plate; **P**, palpus; **pT**, pectinate lamella. Scale bars: A, 500 µm; B, 800 µm; C, 20 µm; D, 30 µm.

Thoracic shield: surface structured like those of tergites (Fig. 24A).

Tergites: posterior paratergite margins projecting slightly posteriorly, in last 2 paratergites almost straight (Fig. 24A).

Endotergum: internal section with short spines and isolated bristles. One row of large circular cuticular pattern between marginal ridge and internal area (Fig. 29A, C, D). External 1 row of marginal bristles, standing closely to one another. Bristles scaly (Fig. 29B), protruding 1/2-2/3 towards posterior margin (Fig. 29A).

Anal shield: well-rounded, neither bell-shaped nor tapered (Figs 24A; 25A; 26A). Like tergites completely covered with numerous, small, irregular pits. Underside carrying 2 well-developed black locking carinae on both sides, anterior 1 small, but well-developed, projecting posteriorly slightly towards anal shield margin. Posterior carina more than 4.5 times longer than first, straight. Locking carinae separated from one another by a distance equal to 1/3 of shorter carina length (Figs 24D; 25D; 26C).

Legs: first tarsi with 4-6, second with 6-8, third with 8 or 9 long ventral spines. First 2 tarsi with weakly curved claws and without apical spine. Tarsi 3-21 with curved claws, 9-12 ventral spines and an apical spine. Ventral spines dispersed through whole inner margin of tarsus. Ninth leg femur 2.3 times longer than wide, tarsi 6.1 times longer than wide. Femora with crenulated ridge of medium length (Figs 24C; 25B).

Stigma-carrying plate: first stigma-carrying plate lobe long and well-rounded, surmounting apical edge of coxa 1. Lobe curved towards coxa, broad and slimmer at pointed tip (Figs 24B; 25C; 26B).

Female sexual characters: only immature females available. Subanal plate with a washboard consisting of well-developed stridulation ribs, 2 ribs on each side. Stridulation ribs symmetrical, broad. Ribs short, ending far away from posterior margin (Fig. 24F). Vulva small, covering fewer than 1/2 of coxa. Operculum low, ending before apical coxa margin. Apical margin of operculum medially weakly notched, with 2 rounded lateral tips (Fig. 24E). Inner plate reaching up to 1/3 operculum height (Fig. 24E).

Male sexual characters: male gonopore covered with single, large, sclerotized, undivided and rounded plate. Apical part of plate membranous. Gonopore covering 1/3 of coxal height and more than 1/2 of coxal width (Fig. 24G). Anal shield well-rounded.

Anterior telopods: first joint with a stridulation harp and two stridulation ribs. Both ribs straight and well-developed. Inner rib reaching only 2/3 of lateral rib length (Fig. 24H). Second joint on posterior side with lobe like, weakly curved process with rounded edges (Fig. 24I, J), protruding almost as high as third joint. Process towards third joint apically with sclerotized spots (Fig. 24J). Tip of third joint strongly bending inwards, protruding twice as high as second joint process. Joint with a cavity juxtaposed to second joint process. Apical margin of third joint well-rounded, towards cavity with numerous sclerotized spots and 2 spines. Two additional spines located closely to tip (Fig. 24I, J). Syncoxite on both sides with only few, isolated hairs (Fig. 24H).

Posterior telopods: third joint weakly curved, becoming slightly slimmer towards tip (Fig. 24K). Hollowed-out margin towards second joint with 3 sclerotized spines (Figs 24K; 25H; 26G), on posterior aspect with one row of *c.* 6 sclerotized teeth (Figs 24L; 25G; 26H). Second joint process slim, almost as long as third joint, tip weakly curved. Anterior side of second joint process basally with one short sclerotized spine. Third joint on both sides basally with some hairs, on rest of surface hairs absent. Second joint on backside almost completely covered with long hairs, anterior side only basally with some long hairs. First joint on both sides with some hairs around its margin (Fig. 24K, L). Inner horns of syncoxite apically curved posteriorly. Tips sharp, whole horns covered with numerous small hairs.

INTRASPECIFIC VARIATION

Smaller specimens show almost no cavity on last joint of anterior telopods. Particularly in the small types of *S. imbecillum* the posterior telopods are slightly slimmer than in larger males (Fig. 25E, F). A variation of the tip of the first stigma-carrying plate (Figs 25C; 26B) is visible, but to few material is

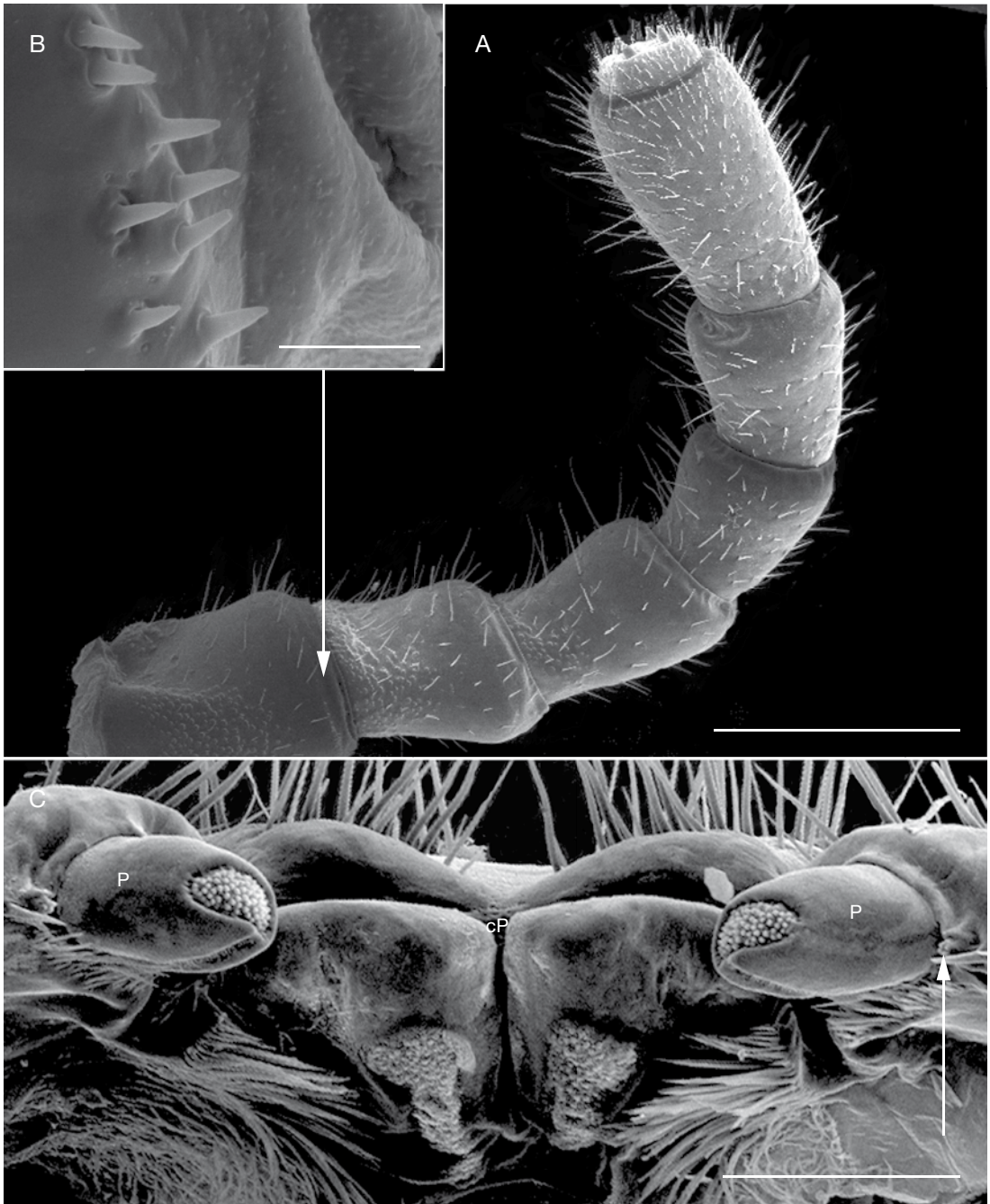


FIG. 28. — *Zoosphaerium voeltzkowianum* (de Saussure & Zehntner, 1897), SEM (BLF 8000): **A**, right antenna, overview; **B**, right antenna, sensory (?) cones on first joint; **C**, gnathochilarium, apical view, arrow marks sensory cones lateral of right palpus. Abbreviations: **cP**, central pads; **P**, palpus. Scale bars: A, 800 µm; B, 30 µm; C, 300 µm.

available to make further studies on the intraspecific variation of this character.

DISTRIBUTION AND ECOLOGY

Only known from the island of Nosy Bé (Fig. 23). Species collected together with two other species of *Zoosphaerium*.

CONSERVATION

The protection status of this species, obviously endemic to Nosy Bé (Fig. 23), is unknown.

REMARKS

The synonymization of *S. imbecillum* and *S. globulus* with *Z. voeltzkowianum* was a difficult task, which needs a longer explanation. The correct identification of this species was not easy, because most of the specimens in the type series were immature, especially all specimens of *S. imbecillum*. The only existing specimen of *S. globulus* is furthermore in poor condition. Type series of both species did not include female specimens and the female specimen of *Z. voeltzkowianum* are obviously immature. The species were distinguished in the original description using the different size and surface structures on tergites as separating characters. The authors do not agree with this conclusion. De Saussure & Zehntner (1902) even observed the striking similarity in the telopods of *S. imbecillum*, *S. globulus* and *Z. voeltzkowianum*. The authors observed furthermore striking similarities in the structure of the endotergum (Fig. 29). All differences mentioned by de Saussure & Zehntner (1897, 1901, 1902) can be explained with the different size of specimens. To make this issue even more complicated, the specimens determined as *Sphaerotherium voeltzkowianum* at the Senckenberg Institute and one female in the type series at the MNHN are not conspecific with the other two males and two females of the type series. In fact, these three specimens may even represent an undescribed genus different from *Zoosphaerium*. *Sphaerotherium imbecillum* and *S. globulus* were described in the same article (de Saussure & Zehntner 1902). In the text and the determination key, *S. globulus* is mentioned at first, but the plates of *S. imbecillum* and *Z. voeltzkowianum* were published five years before the publication

of the description in 1897 (see Jeekel 1999 for a statement about this issue). Because of these facts, *S. globulus* and *S. imbecillum* are both proposed to be synonymous to *Z. voeltzkowianum*.

Zoosphaerium platylabum species-group

SPECIES INCLUDED. — *Zoosphaerium platylabum* (de Saussure & Zehntner, 1897).

DISTRIBUTION. — Unclear, since most species are still undescribed.

DIAGNOSIS. — This species group is still monotypic, but numerous undescribed species close to *Z. platylabum* were discovered, justifying its establishment. The characters unifying this group are unique in Sphaerotheriida.

All species have 2 locking carinae on the ventral side of the anal shield. The carinae are located more closely to the laterotergites than towards the anal shield margin (Fig. 30E). The operculum of female vulva is protruding into 2, sharp edged processes. (Fig. 30F). A phylogenetic analysis will be necessary to confirm if the *platylabum*-group represents a monophyletic group to be kept separately from the other Malagasy sphaerotheriids.

Zoosphaerium platylabum (de Saussure & Zehntner, 1897) (Figs 30-33)

Sphaerotherium platylabum de Saussure & Zehntner, 1897: pl. 5, fig. 9; 1902: 54, pl. 15, fig. 5. — Attems 1910: 86, pl. 10, figs 5-8.

Sphaerotherium (Globotherium) platylabum – Brolemann 1922: 234, fig. 9.

Zoosphaerium platylabum – Jeekel 1999: 13 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — Madagascar, province Antananarivo, Antananarivo (Tanarive), 1890, leg. Catat, ♂ holotype (damaged, anterior telopods missing) (MNHN CB041).

OTHER MATERIAL EXAMINED. — **Madagascar.** Leg. Lantz, 160-1882, 1 ♂ (MNHN n° 30). — Parc national Andasibe, 23 road km E Moramanga, 960 m, rainforest, 18°56'38"S, 48°25'03"E, general collecting at night, coll. C. Griswold, D. Silva, D. Andriamalala, 16-18.I.2003, 1 ♂ (BLF 7994). — Andasibe, sous-préf. Moramanga, réserve Analamazoatra (Perinet), forêt primaire, 960-1020 m, 21.XI.1989, coll. C. Lienhard, 1 ♂, 1 ♀ (MHNG Mad89/5).

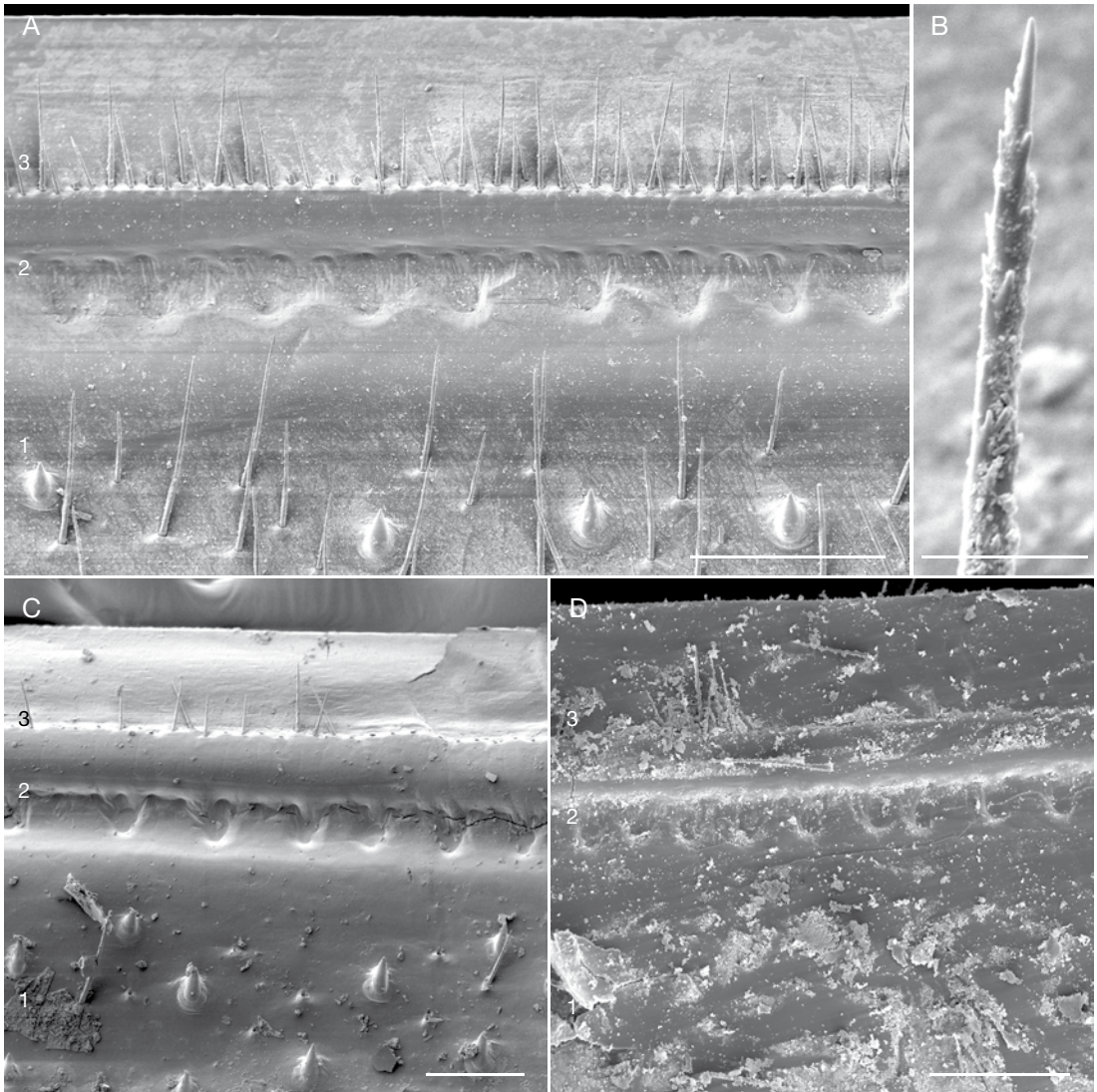


FIG. 29. — *Zoosphaerium voeltzkowianum* (de Saussure & Zehntner, 1897), SEM, endotergum of midbody tergite: **A**, overview (lectotype); **B**, marginal bristle, detail (lectotype); **C**, overview (paralectotype of *Z. imbecillum* n. syn.); **D**, overview (holotype *Z. globulus* n. syn.). Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section. Scale bars: A, D, 200 μ m; B, 10 μ m; C, 100 μ m.

DIAGNOSIS. — Medium sized giant pill-millipede (Fig. 30A). Colour in alcohol yellow-greenish, surface of tergites and anal shield almost completely covered with small pits and hairs. First antennomere with single joint (Fig. 31A), joints 1-5 with sclerotized teeth (Fig. 31A, B). Apical joint with 36-41 sensory cones (Fig. 31C). Third joint of posterior telopods remarkably thick (only 1.3 times longer than wide) with stout tip

(Fig. 30K, L), on posterior and anterior side with single row of sclerotized spots. Anterior telopod with single long, strong stridulation rib and an elongated third joint (Fig. 30H-J). Anal shield not bell-shaped but with steep slope (Fig. 30A). Two well-developed black locking carinae on each side of the anal shield, posterior carina short, only 1.5 times longer than anterior carina (Fig. 30E). First stigma-carrying plate with one long

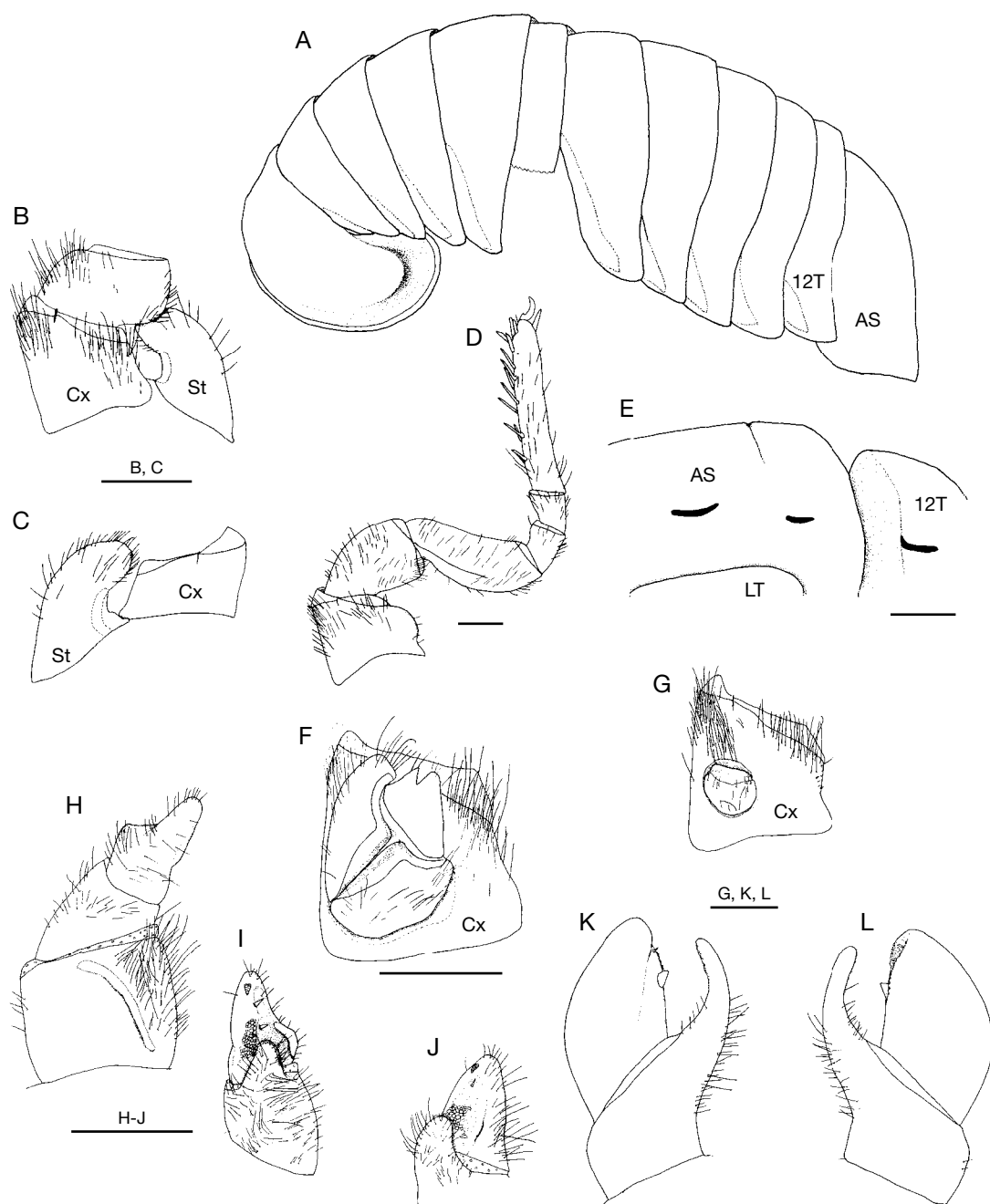


FIG. 30. — *Zoosphaerium platylabum* (de Saussure & Zehntner, 1897): **A-E, K, L**, holotype; **A**, habitus, body length 36 mm; **B, C**, coxa and prefemur of 1st right leg with 1st stigma-carrying plate; **B**, posterior view; **C**, anterior view; **D**, 9th left leg; **E**, closing ledges of anal shield; **F**, coxa of second left leg with vulva, posterior view (♀ MNHG); **G**, coxa of 2nd left leg with gonopore (BLF 7994); **H-J**, right anterior telopod (BLF 7994); **H**, anterior view; **I**, joints 2 and 3, posterior view; **J**, joints 2 and 3, inner view; **K, L**, last two joints of right posterior telopod; **K**, anterior view; **L**, posterior view. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **LT**, laterotergite; **St**, stigma-carrying plate. Scale bars: B-L, 1 mm.

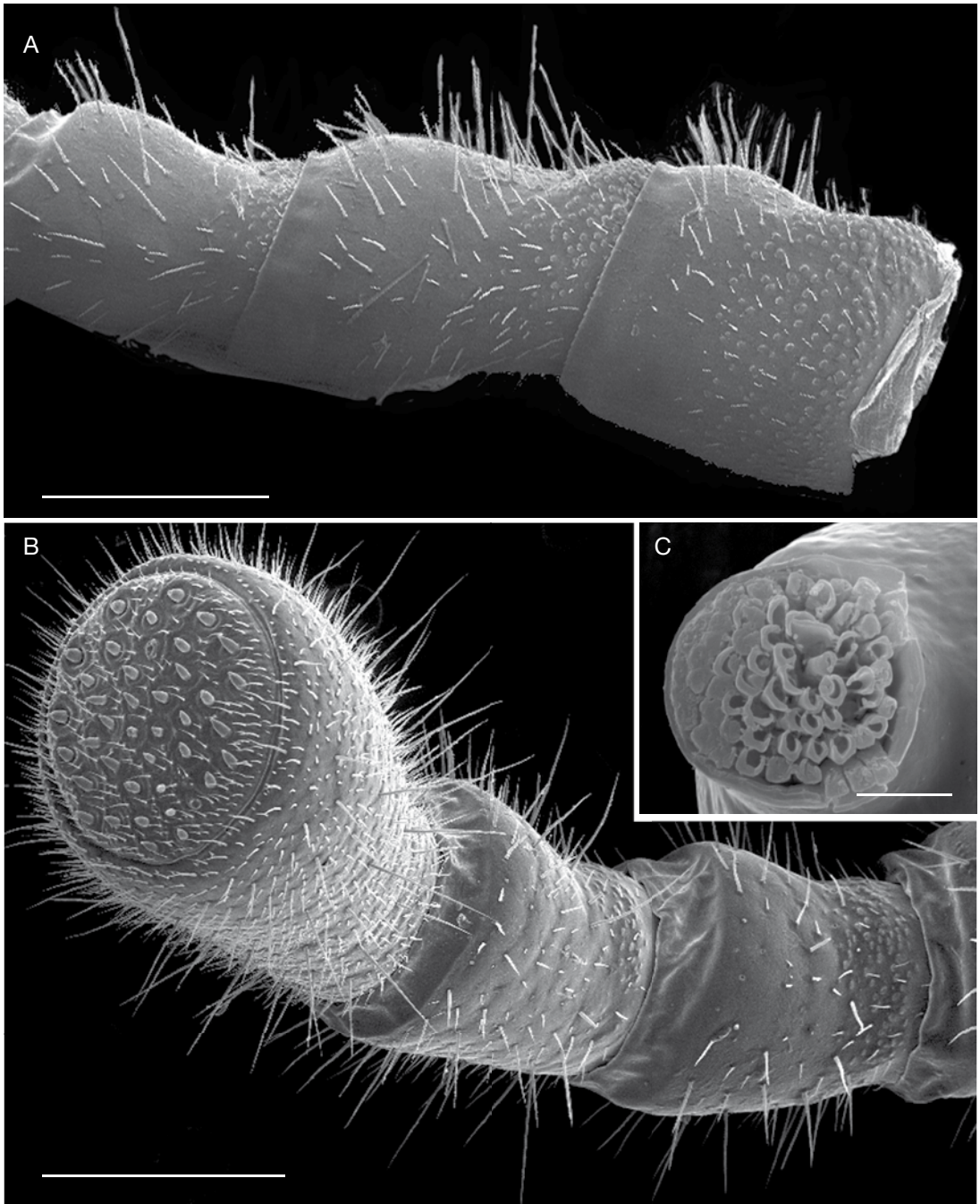


FIG. 31. — *Zoosphaerium platylabum* (de Saussure & Zehntner, 1897), SEM, right antenna, lateral view (BLF 7994): **A**, joints 1-3; **B**, joints 4-6; **C**, detail of tip of 6th joint sensory cone. Scale bars: A, 1 mm; B, 800 µm; C, 6 µm.

and broad lobe (Fig. 30B, C). Female subanal plate on each side with single broad and strong stridulation rib. Operculum of female vulva notched, protruding into two sharp edged processes, lateral process wider than inner one (Fig. 30F).

SIMILAR SPECIES

The thick third joint of posterior telopods and the large, long, well-rounded lobe of the first stigma-carrying plate identifies this species unambiguously.

DESCRIPTION

Body measurements: male (holotype only) length up to 36.35, width of thoracic shield up to 19.65, height of thoracic shield up to 9.9. Female: length up to 40.9, width up to 23.9, height up to 11.35.

Habitus: body in comparison to other Malagasy Sphaerotheriida slightly elongated (Fig. 30A).

Coloration: tergites (in alcohol) yellowish to light green. Collum, head, antennae and legs dark green.

Head: posterior margin of head towards collum without patch of small hairs.

Antennae: length of joints: $1 > 2 > 3 = 4 = 5 < 6$, sixth joint longest, of cylindrical shape (Fig. 31A, B), apically with one row of sensilla basiconica, on tip bearing a disc with 36–41 sensory cones (Fig. 31B, C). First joint remarkably broader than others, short and with single groove (Fig. 31A). Sclerotized teeth at base of joints 1–5, not reaching apical border (Fig. 31A). First joint without sensilla basiconica.

Mandible: with 6 rows of pectinate lamellae, number of teeth decreasing proximad (Fig. 33A). Condylus with 1 strongly developed step near apical margin (Fig. 33A).

Gnathochilarium: ventral side with numerous bristles (Fig. 32A). Four sensory cones, located together lateral of palpi (Fig. 32B). Two different types of sensory uvulae on central pads: long, cylinder-shaped ones with 1 medial pit and plain ones without pit.

Collum: anterior and posterior margin with some long, isolated hairs. Few isolated hairs on remaining part of collum

Thoracic shield: surface glabrous (Fig. 30A).

Tergites: especially anteriorly covered completely with small pits, each support a short hair.

Endotergum: internal section with short spines and isolated bristles (Fig. 33B). One row of elliptical grooves, distance between those impressions larger than their diameter (Fig. 33B). External 2 rows of marginal bristles placed closely to one another. Bristles scaly (Fig. 33C), short, reaching $1/2$ – $2/3$ towards area between basal point of bristles and posterior tergite end (Fig. 33B).

Anal shield: not bell-shaped or tapered (Fig. 30A). Surface like tergites completely covered with numerous small pits, each supporting a short hair. Ventral side with 2 black locking carinae on both sides, anterior one similar to those of tergites, posterior carina small, 1.5 times longer than first (Fig. 30E). Both carinae almost parallel to margin, located closely towards last pair of laterotergites. Locking carinae separated from each other by a distance equal to double length of shorter carina (Fig. 30E).

Legs: first tarsi in type specimen with four, second with 5–7, third pair with 8 or 9 ventral spines. First 2 tarsi with weakly curved claws and without apical spine. Tarsi 3–21 with curved claws, 12–14 ventral spines and an apical spine. Ventral spines dispersed on whole inner side of tarsus (Fig. 30D). In 9th leg femur 2.3 times longer than wide, tarsi 5.8 times longer than wide. Femora with single, long crenulated ridge (Fig. 30D).

Stigma-carrying plate: first stigma-carrying plate lobe long, curved strongly towards coxa, protruding above mid-length point of prefemur (Fig. 30B, C). Lobe long, extraordinary broad with one well-rounded tip (Fig. 30C).

Female sexual characters: subanal plate with a washboard, consisting of a single well-developed stridulation rib on each side. Stridulation rib symmetrical and of medium length. Vulva large, covering more than $2/3$ of coxa (Fig. 30F). Operculum medially notched, with 2 pointed tips. Both tips reaching same height, but lateral one twice as wide as inner tip (Fig. 30F). Inner plate long and broad, protruding almost as high as operculum (Fig. 30F).

Male sexual characters: male gonopore covered with 1 large, sclerotized, undivided and rounded plate. Apical part of plate membranous. Gonopore covering $1/3$ of height and slightly less than $1/2$ of

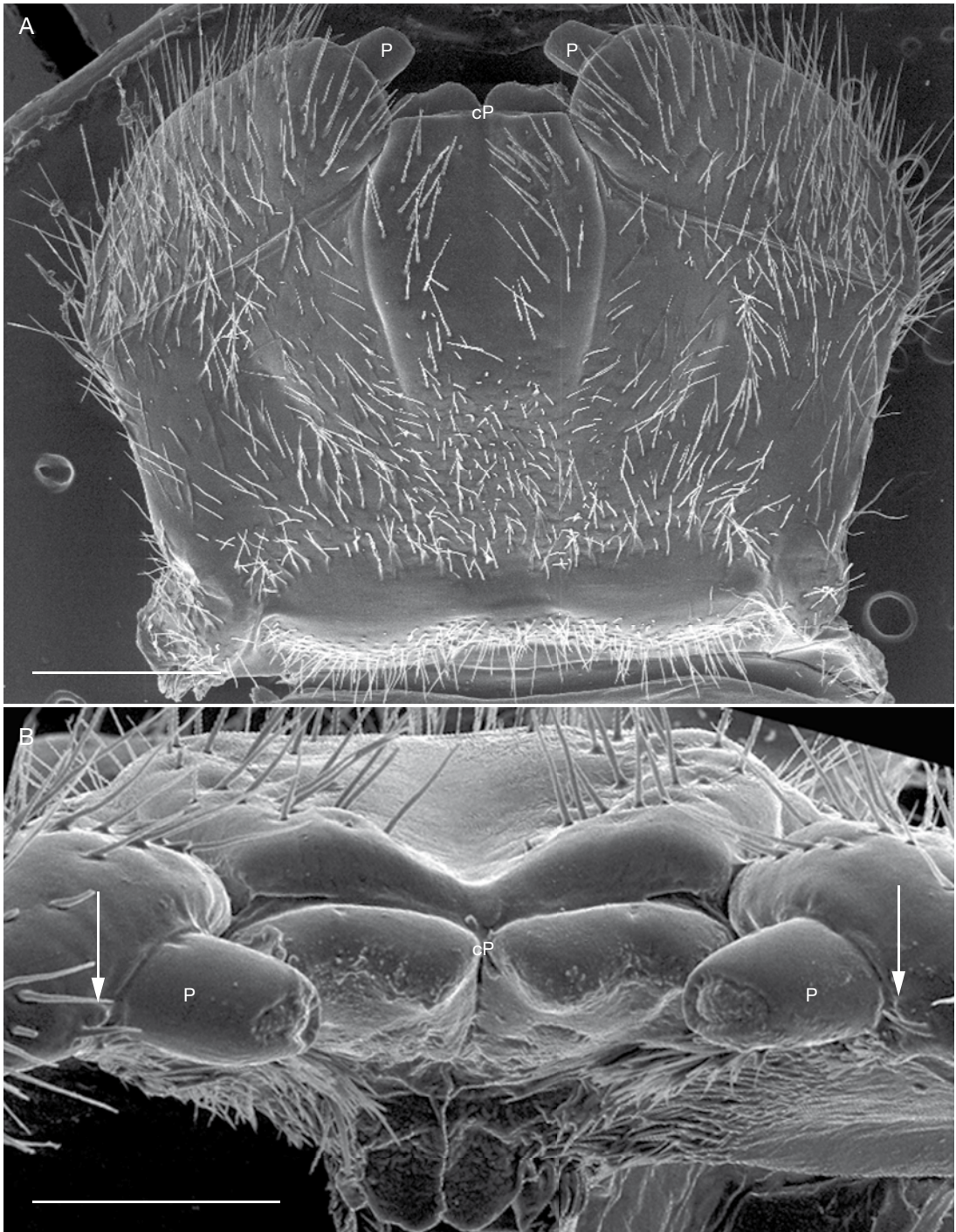


FIG. 32. — *Zoosphaerium platylabum* (de Saussure & Zehntner, 1897), SEM, gnathochilarium (BLF 7994): **A**, anterior side; **B**, apical view, arrows indicate the positions of sensory cones lateral of palpi. Abbreviations: **cP**, central pads; **P**, palpus. Scale bars: A, 1 mm; B, 500 μ m.

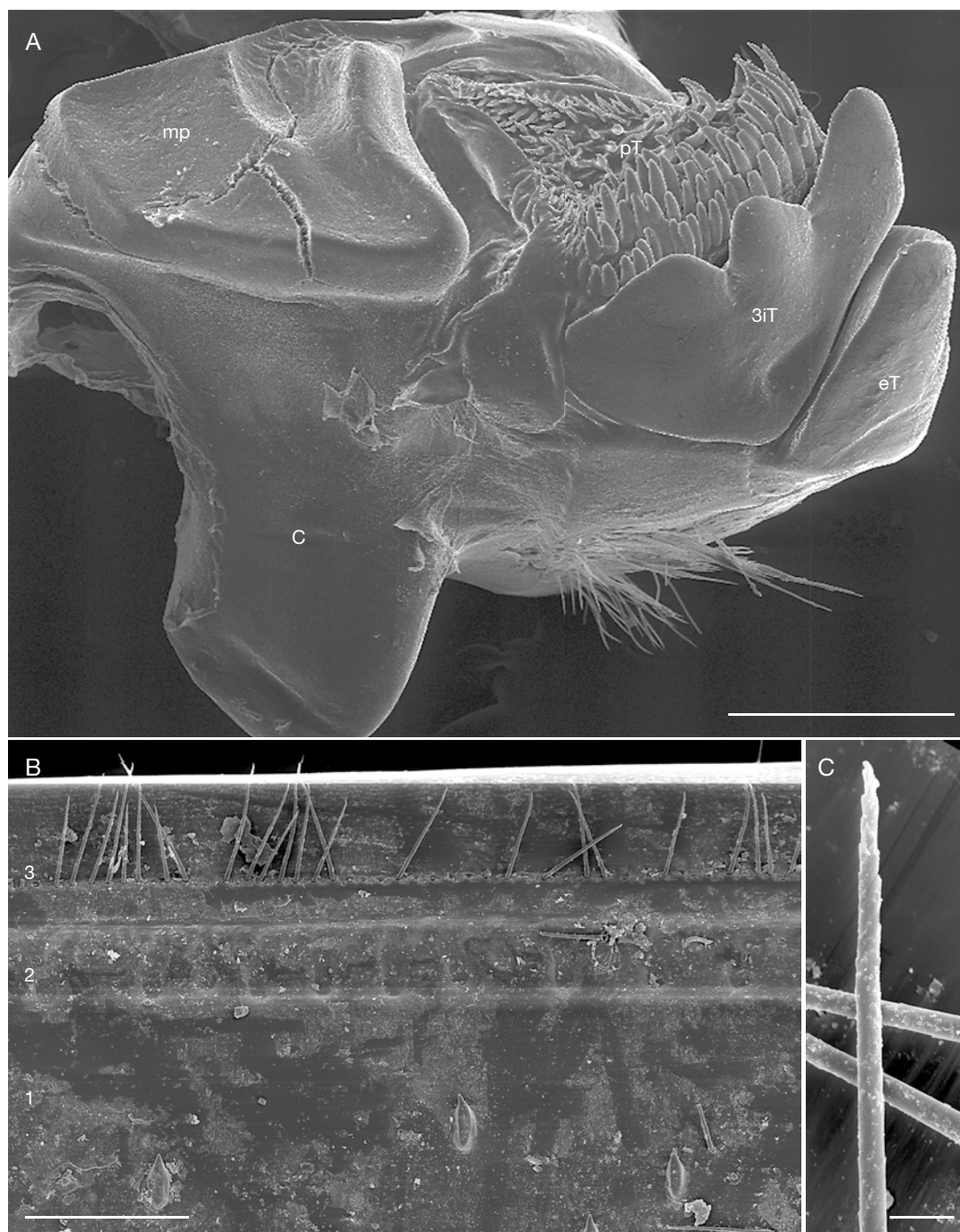


FIG. 33. — *Zoosphaerium platylabum* (de Saussure & Zehntner, 1897), SEM: **A**, right mandible, overview (BLF 7994); **B**, endotergum of midbody tergite (holotype); **B**, overview; **C**, marginal bristle, detail. Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section; **3iT**, 3 internal teeth; **C**, condylus; **eT**, external tooth; **mp**, molar plate; **pT**, pectinate lamella. Scale bars: A, 600 μ m; B, 200 μ m; C, 7 μ m.

coxal width (Fig. 30G). Anal shield completely covered with hair and with steep slope (Fig. 30A).

Anterior telopods: syncoxite on both sides without hair, but on anterior side covered with numerous, small, triangular black spines. First joint with a stridulation harp and one long, broad and strong stridulation rib (Fig. 30H). Second joint on posterior side with one lobe-like, weakly curved process with rounded edges (Fig. 30I, J). Point of process protruding not as high as midpoint of third joint, towards third joint apically with sclerotized spots (Fig. 30J). Third joint elongated, of cylindrical shape, protruding internally much higher than laterally. Joint with a cavity juxtaposed to second joint. Inner side of cavity with numerous sclerotized spots, lateral side with 3 spines (Fig. 30I, J). A single sclerotized tooth located closely to tip (Fig. 30I).

Posterior telopods: third joint conspicuously enlarged (1.2 times longer than wide), joint ending in a stout tip. Towards second joint with a hollowed-out margin carrying 1 large, blunt membranous lobe and 2 short spines (Fig. 30K). Anterior aspect with one row of minute sclerotized spots located at margin closely towards tip. Posterior aspect of third joint with *c.* 19 small sclerotized teeth (Fig. 30L). Process of second joint slim and shorter than third joint, with strongly arched tip. Anterior side apically with some sclerotized spots juxtaposed to third joint (Fig. 30K). Third joint glabrous, second joint on both sides marginally with some long, isolated hairs (Fig. 30K, L), first joint on both sides glabrous.

INTRASPECIFIC VARIATION

The specimen of the BLF 7994 has more ventral spines (8) at the first pair of legs. It shows the same number of sclerotized teeth on the posterior telopods.

DISTRIBUTION AND ECOLOGY

The only locality where recent material of *Z. platylabum* was collected is the rainforest at PN Andasibe (Fig. 41). The relatively plenty records in the literature (Attems 1910; Brolemann 1922) may indicate, that this species has (or had?) a wider distribution. The CAS specimen was in the same vial with an immature female of an undescribed *Zoosphaerium* species.

CONSERVATION

This species is conserved in the Parc national Andasibe (Fig. 41).

Zoosphaerium piligerum species-group

SPECIES INCLUDED. — *Zoosphaerium piligerum* (de Saussure & Zehntner, 1897).

DISTRIBUTION. — Unclear, since most species are undescribed.

DIAGNOSIS. — This species group is still monotypic. Several undescribed species close to *Z. piligerum* were discovered, justifying the establishment of this species-group. The third joint of posterior telopods is slim and strongly elongated (Fig. 34J). Process of second joint is long, slender and curved towards the third joint (Fig. 34K). Similarities can also be found on the anterior telopods (Fig. 34G-I). A phylogenetic analysis will be necessary to confirm if the *piligerum*-group represents a monophyletic group to be kept separately from the other Malagasy sphaerotheriids.

Zoosphaerium piligerum

(de Saussure & Zehntner, 1897)

(Figs 34-37)

Sphaerotherium piligerum de Saussure & Zehntner, 1897: pl. 5, figs 19-19a; 1902: 36, pl. 15, figs 4-4b.

Zoosphaerium piligerum – Jeekel 1999: 11 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — Madagascar, I.1890, leg. Catat, ♂ holotype (MNHN CB040).

OTHER MATERIAL EXAMINED. — **Madagascar.** Province Antananarivo, 3 km 41° NE Andranomay, 11.5 km 147° SSE Anjozorobe, 18°28'24"S, 47°57'36"E, 1300 m, montane rainforest, 5-13.XII.2000, coll. Griswold *et al.*, general collecting, 1 ♂, 3 ♀♀ (BLF 2543); 1 ♀ (BLF 2371); 1 ♀ (BLF 2377).

DIAGNOSIS. — Up to 53 mm long. Colour splendid blackish (Fig. 19B), younger individuals darkish green. Surface of tergites shiny, with few, small isolated hairs. Anal shield bell-shaped, in the male covered completely with short hairs, in the female with few small hairs. Antennomere 1-2 with sclerotized teeth (Fig. 35A). Apical joint with 12-19 sensory cones (Fig. 35B). All antennal joints without groove (Fig. 35A, B). Posterior telopod third joint strongly curved, posterior side with up to 14 sclerotized teeth, a large, non-sclerotized lobe (Fig. 34K)

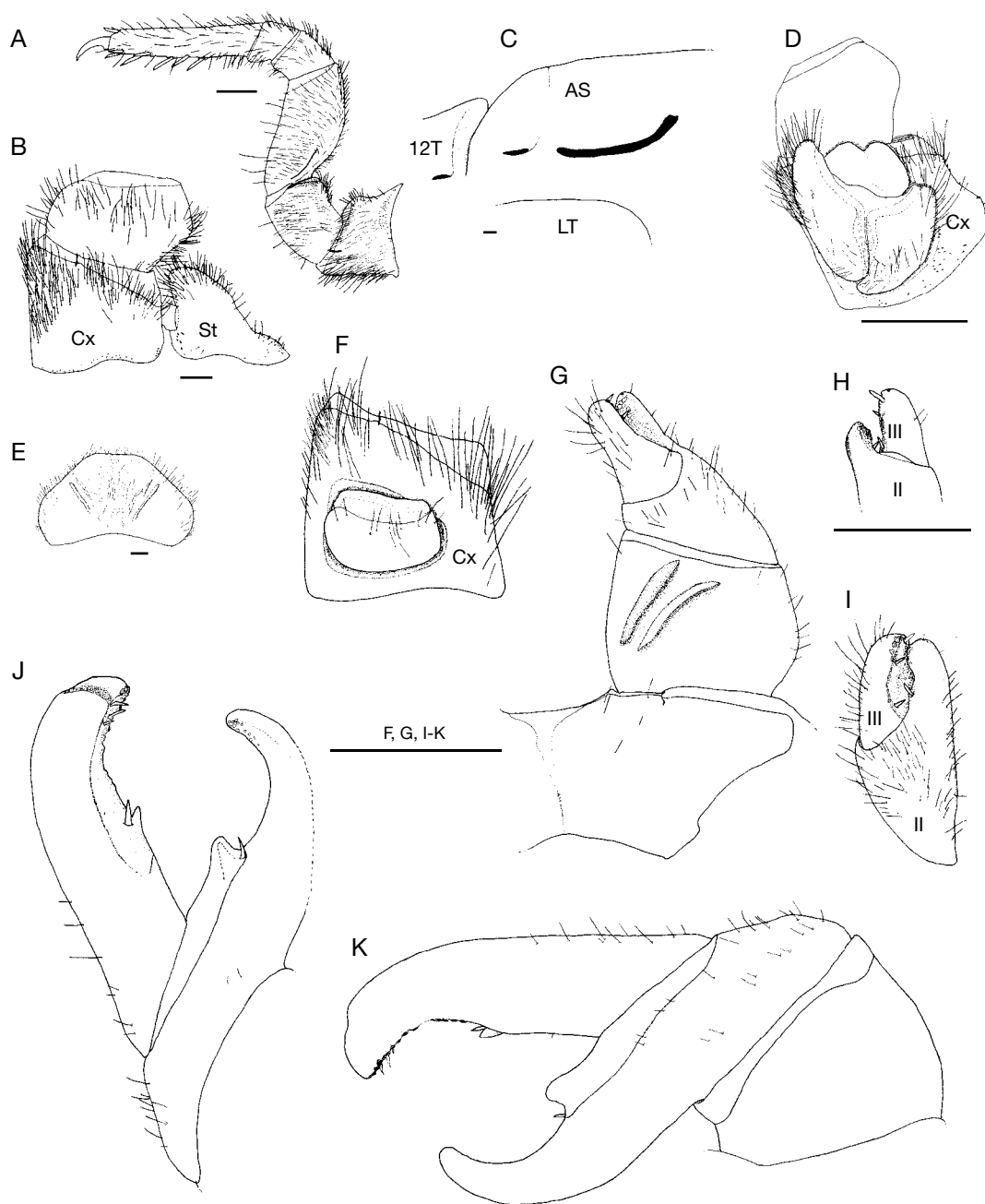


FIG. 34. — *Zoosphaerium piligerum* (de Saussure & Zehntner, 1897): **A, B, D-F, J, K**, specimen BLF 2543; **C, G-I**, holotype; **A**, 9th left leg; **B**, coxa and prefemur of 1st right leg with 1st stigma-carrying plate; **C**, closing ledges of anal shield; **D**, coxa and prefemur of 2nd left leg with vulva; **E**, subanal plate; **F**, coxa of 2nd left leg with gonopore; **G-I** right anterior telopod; **G**, anterior view; **H**, inner view; **I**, lateral view; **J, K**, left posterior telopod; **J**, joints 2 and 3, anterior view; **K**, posterior view. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **LT**, laterotergite; **St**, stigma-carrying plate. Scale bars: 1 mm.

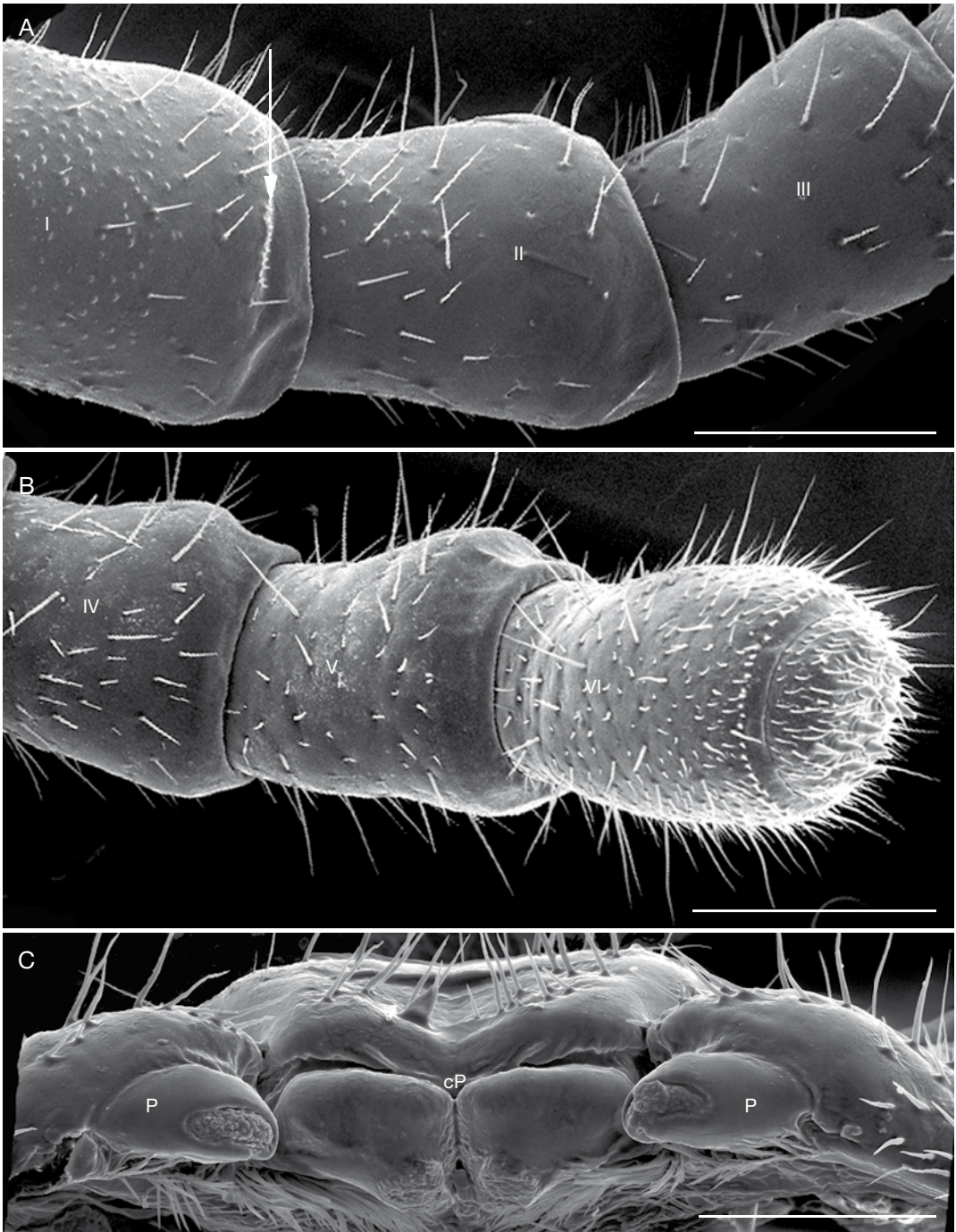


FIG. 35. — *Zoosphaerium piligerum* (de Saussure & Zehntner, 1897), SEM (BLF 2543): **A**, **B**, right antenna; **A**, ventral view, joints 1-3, arrow marks position of short sensorial hairs on first joint; **B**, lateral view, joints 4-6; **C**, gnathochilarium, apical view. Abbreviations: **cP**, central pads; **P**, palpus. Scale bars: A, 600 μ m; B, 500 μ m; C, 400 μ m.

and around 4 sclerotized spines. Second joint with long and slim immovable digit, strongly curved, basally with one large membranous lobe and a spine. Two stridulation ribs on male harp (Fig. 34G) and 1 or 2 on each side of female washboard (Fig. 34E). Anal shield with 2 locking carinae, first small, second 3–4 times longer than first (Fig. 34C). Operculum large, surmounting coxa, apically with 2 well-rounded lobes protruding to same height. Interior plate of vulva surmounting operculum (Fig. 34D).

SIMILAR SPECIES

The shape of posterior telopods is unique for described Malagasy Sphaerotheriida.

DESCRIPTION

Body measurements: males (2 specimens): length up to 36.0, width of thoracic shield up to 13.45, height of thoracic shield up to 7.85. Females (4 specimens): length up to 52.45, width up to 24.65, height up to 13.3.

Habitus: tergites shiny and with few hairs. At high magnification small isolate pores and a leather-like surface become visible.

Coloration: tergites splendid blackish (Fig. 19B). Head, antennae and legs dark olive-greenish.

Head: posterior margin of head towards collum with patch of small hairs.

Antennae: length of joints: $1 < 2 < 3 > 4 = 5 < 6$, sixth joint longest, of cylindrical shape (Fig. 35A, B), apically with one row of sensilla basiconica, on tip bearing a disc with 12–19 sensory cones (Fig. 35B). First joint remarkably broader than the others, short and without groove (Fig. 35A). Sclerotized teeth at base of joints 1–2, not reaching apical border (Fig. 35A). First joint apically on one side with 1 or 2 rows of sensilla basiconica (Fig. 35A).

Mandible: with 6 rows of pectinate lamellae, number of teeth decreasing proximad (Fig. 36B). Condylus with 2 steps near apical margin, proximal step strongly developed, apical step barely visible.

Gnathochilarium: ventral side with few bristles (Fig. 36A). No sensory cones visible lateral of palpi (Fig. 35C). Two different types of sensory uvulae on central pads: long, cylinder-shaped ones with single medial pit and more plain ones without pit.

Collum: anterior and posterior margin each with c. 16 long hairs arranged in a single row. Remaining parts of collum glabrous.

Thoracic shield: glabrous, but lateral extensions especially at margins with patch of long hairs.

Tergites: tips of paratergites posterior margin projecting posteriorly. Tergites smooth and with few, small isolated hairs.

Endotergum: internal section with short spines and isolated bristles. One row of elliptical cuticular patterns, standing in a small distance towards one another between marginal ridge and internal area (Fig. 37). External 2 (in rare exceptions three) rows of marginal bristles, placed closely to one another. Bristles slightly surmounting posterior end of tergite (Fig. 37).

Anal shield: bell-shaped. In contrast to the almost glabrous and polished tergites with numerous hairs. Underside carrying 2 well-developed black locking carinae on both sides, anterior one small, posterior carina 4 times longer than first, at posterior end slightly projecting towards anal shield margin (Fig. 34C). Locking carinae separated from each other by a distance equal to the length of shorter carina (Fig. 34C).

Legs: first tarsi with up to 4, second with up to 5, third pair with 6–8 long ventral spines. First two tarsi with only weakly curved claws and without apical spine. Tarsi 3–21 with curved claws, 7–10 ventral spines and an apical spine. Ventral spines dispersed through whole inner margin of tarsus (Fig. 34A). In 9th leg, femur 1.8 and tarsi 4.8 times longer than wide (Fig. 34A).

Stigma-carrying plate: first stigma-carrying plate lobe short and stout, protruding up to apical edge of coxa 1. Lobe only weakly curved towards coxa, broad, stout tip only a little thinner than more basal parts (Fig. 34B).

Female sexual characters: subanal plate with a washboard, consisting of well-developed stridulation ribs, 1 or 2 on each side. Stridulation ribs symmetrical, sometimes non-continuous. Ribs long, ending shortly before posterior margin of plate (Fig. 34E). Vulva large, covering more than 4/5 of coxa (Fig. 34D). Operculum surmounting coxa. Operculum medially notched with 2 rounded lateral tips, both protruding to same height (Fig. 34D). Inner plate extraordinary long and broad, surmounting operculum (Fig. 34D).

Male sexual characters: male gonopore large, covered with one sclerotized, undivided and rounded

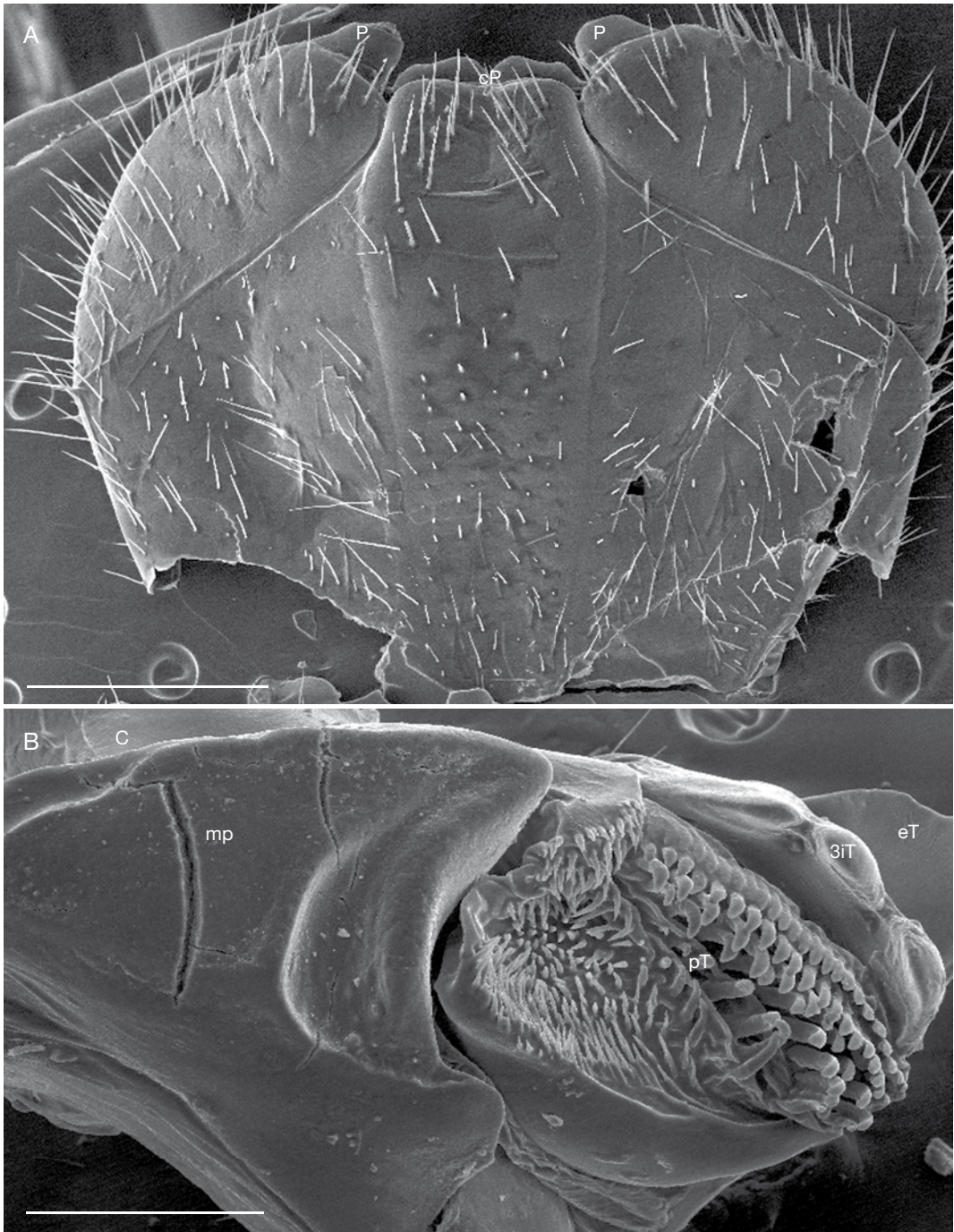


FIG. 36. — *Zoosphaerium piligerum* (de Saussure & Zehntner, 1897), SEM (BLF 2543): **A**, gnathochilarium, overview; **B**, left mandible, pectinate lamella and molar plate. Abbreviations: **3iT**, 3 internal teeth; **C**, condylus; **cP**, central pads; **eT**, external tooth; **mp**, molar plate; **P**, palpus; **pT**, pectinate lamella. Scale bars: A, 800 μ m; B, 400 μ m.

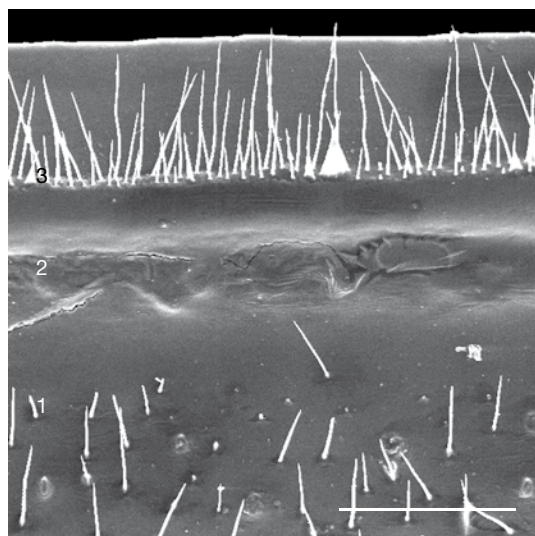


FIG. 37. — *Zoosphaerium piligerum* (de Saussure & Zehntner, 1897), SEM (BLF 2543), endotergum of midbody tergite, overview. Abbreviations: 1, endotergum, internal section; 2, endotergum, medial section; 3, endotergum, external section. Scale bar: 400 μ m.

plate. Apical part of plate membranous. Gonopore covering 2/5 of coxal height and more than 1/2 of coxal width (Fig. 34F). Anal shield bell-shaped and completely covered with numerous small hairs.

Anterior telopods: first joint with a stridulation harp and two stridulation ribs. Both ribs straight and of same length (Fig. 34G). Second joint on posterior side with single, lobe like, weakly curved process with rounded edges (Fig. 34H, I). Point of process protruding almost as high as third joint, towards third joint apically with sclerotized spots and basally with spine (Fig. 34H). Third joint almost as wide as process of second joint, of cylindrical shape with well-rounded apical margin. Juxtaposed to process of second joint with a cavity. Margin towards cavity with 5 sclerotized teeth, numerous sclerotized spots and 3 small spines. Spines located basally, medially and the largest one apically close towards tip (Fig. 34G-I).

Posterior telopods: third joint strongly curved around the suspiciously excavated tip (Fig. 34J, K). Hollowed-out margin towards second joint with 1 large membranous lobe and up to 4 smaller, sclerotized spines, 3 of them located around tip, fourth one

largest and located adjacent to the lobe (Fig. 34J). Third joint on posterior aspect with row of c. 15 crenulated teeth (Fig. 34K). Process of second joint slim and shorter than third joint, with strongly curved tip. Anterior side basally with 1 membranous lobe and 1 sclerotized spine, furthermore on inner margin around tip with numerous small, sclerotized spots juxtaposed to third joint. Third joint only basally with few isolated hairs, hairs absent on rest of surface (Fig. 34J, K). First and second joint almost glabrous, on both sides with some isolated hairs (Fig. 34J). Inner horns of syncoxite apically curved posteriorly. Tips sharp, whole horns covered with numerous small hairs.

INTRASPECIFIC VARIATION

The material contained too few specimens to evaluate the intraspecific variation. Among the material, no variation among the locking carinae and only a little variation among the sensory cones of antenna and ventral spines on the legs were observed. The smaller individuals, including one male specimen, had well-rounded anal shields.

DISTRIBUTION AND ECOLOGY

This species is only known from the montane rainforest at Andranomay (Fig. 41). It is unclear if this species is endemic to this single forest, but it was not found in other samples. At least four other giant pill-millipede species were collected in Andranomay, all of them are undescribed.

CONSERVATION

Because the species is until now only known from the montane forest in Andranomay (Fig. 41), its prospects of survival are directly connected with the survival of this specific habitat. Because of the fast ongoing destruction of the forest ecosystems on Madagascar, *Z. piligerum* may be in urgent threat of extinction.

Species not assignable to a group

The following species could not be placed in a species-group. Nevertheless, when the description of undescribed species proceeds, erecting new species groups would possibly be necessary.

KEY TO SPECIES OF *ZOOSPHAERIUM* NOT ASSIGNABLE TO A GROUP

1. Third joint of posterior telopods with one long, membranous lobe towards second joint. Female vulva large, operculum surpassing coxa *Z. subreflexum*
- Third joint of posterior telopods without long, membranous lobe, joint shorter or as long as second joint. Both joints strongly curved towards one another and with numerous long hairs on both sides (Fig. 38G, H) *Z. blandum*

Zoosphaerium subreflexum Jeekel, 1999

Zoosphaerium subreflexum Jeekel, 1999: 5. — Enghoff 2003: 620 (lists species name).

REMARKS

See Jeekel (1999) for a complete description of this species. The type specimens of this species are stored at the Museum Amsterdam (C. A. W. Jeekel pers. comm.) and were not seen by the present author.

Zoosphaerium blandum

(de Saussure & Zehntner, 1902)

(Figs 38-40)

Sphaerotherium blandum de Saussure & Zehntner, 1902: 63, pl. 15, figs 9-9b, figs 10-10c.

Sphaerotherium stridulator de Saussure & Zehntner, 1902: 66, pl. 15, figs 6-6e n. syn.

Sphaerotherium (Globotharium) blandum – Demange 1969: 485, figs 4-7.

Zoosphaerium blandum – Jeekel 1999: 12 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — *Zoosphaerium blandum*: coll. C. Alluaud, 1901, ♂ holotype (MNHN CB011). *Sphaerotherium stridulator*: coll. C. Alluaud, 1901, ♂ holotype (MNHN CB045).

TYPE LOCALITY. — *Zoosphaerium blandum* and *Sphaerotherium stridulator*: Madagascar, col de Sakavalana (possibly Sakavalana mine), 20°44'48"S, 46°4'30"E.

OTHER MATERIAL EXAMINED. — **Madagascar**. Andrahomana, coll. C. Alluaud, VIII-XI.1900, 1 immature ♂ (MNHN CB011) (maybe Province Toliara, 25°10'60"S, 46°40'0"E, 89 m). — Sud-Ouest, Tulear, coll. I. Bigot, VI.1965, 1 ♂ (MNHN CB011). — 7.5 km ENE Hazofotsy (Réserve naturelle intégrale d'Andohahela camp #6), 24°49.0'S, 46°36.6'E, 120 m, leg. S. Goodman, 7-15.XII.1995, 1 ♂ (FMMC 5372).

DIAGNOSIS. — Up to 23 mm long. Colour faded in alcohol. Surface of tergites smooth and glabrous. Anal shield weakly rounded, with relatively steep slope. Antennomeres 1-3 with sclerotized teeth (Fig. 39A). Apical joint with 4 sensory cones (Fig. 39A). First antennal joint with groove (Fig. 39A). Third joint of posterior telopods of abnormal shape, posterior side with up to 15 sclerotized knobs, a single large lobe and up to 5 sclerotized spines (Fig. 38H). Second joint immovable digit broad and strongly curved towards third joint, basally sometimes with 1 large membranous lobe and a spine (Fig. 38G, I, J). Two stridulation ribs on each male harp (Fig. 38D). Anal shield with 2 locking carinae of variable length, in some specimens the posterior or even both carinae completely absent. Female unknown.

SIMILAR SPECIES

The unusual shape of the chela of posterior telopods in combination with the presence of two stridulation ribs on the harp identifies *Z. blandum* unambiguously.

DESCRIPTION

Body measurements (males, 5 specimens): length up to 22.8, width of thoracic shield up to 10.75, height of thoracic shield up to 6.85.

Habitus: general appearance elongated.

Coloration: tergite coloration in alcohol faded, with mix of brown and greenish. The relatively fresh FMNH specimen shows a much darker coloration on posterior half of tergites. Head, collum, antennae and tips of legs greenish.

Head: posterior margin of head towards the collum without patch of small hairs.

Antennae: length of joints: 1<2>3=4=5<6, sixth joint longest, of cylindrical shape (Fig. 39A), apically with 1 row of sensilla basiconica, on tip bearing a disc with 4 (5) sensory cones (Fig. 39A). First joint remarkably broader than the others, short and with groove (Fig. 39A). Sclerotized teeth at base of joints 1-3, reaching apical border only on first joint (Fig. 39A). First joint apically on one side with 1 or 2 rows of sensilla basiconica (Fig. 39B).

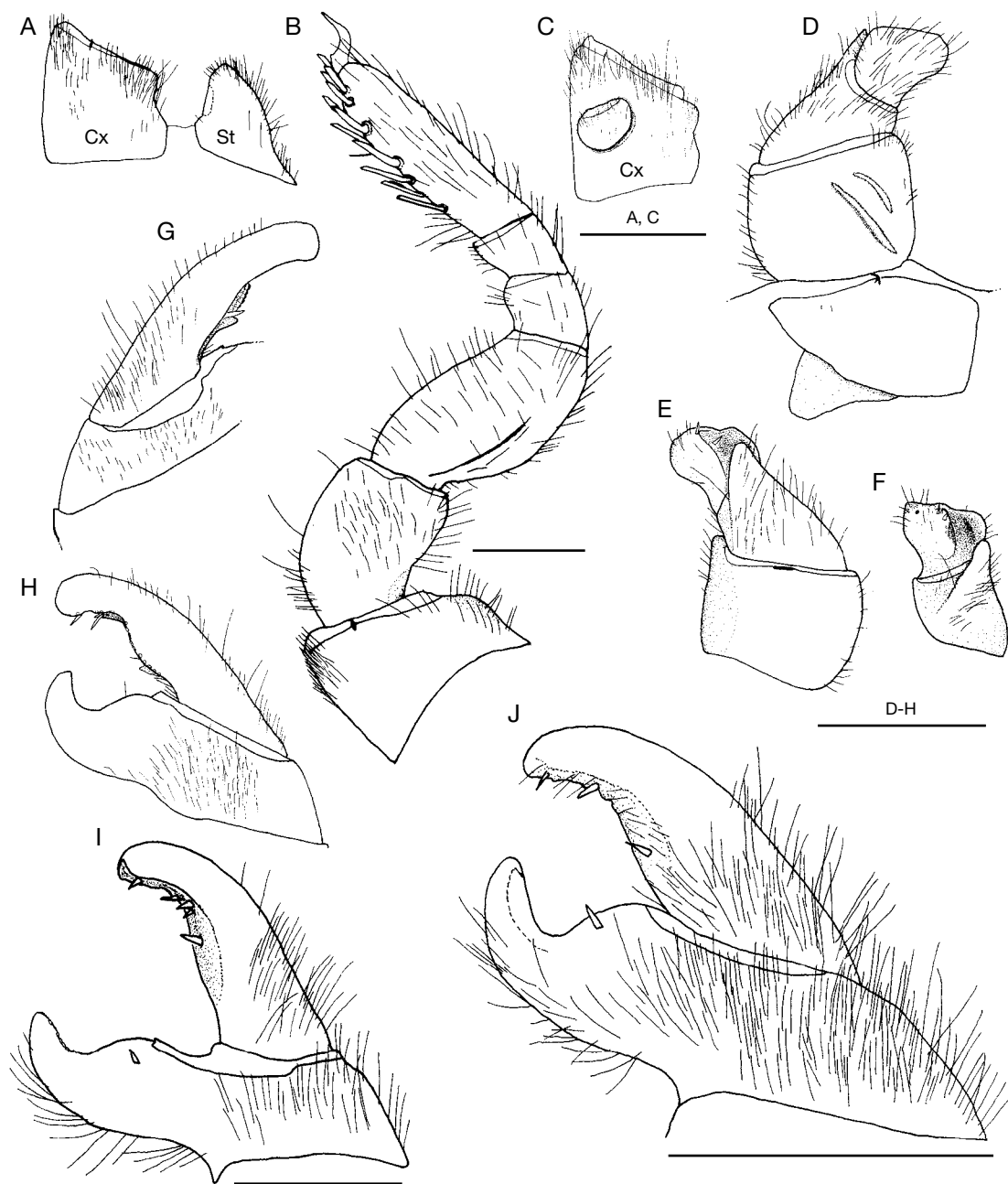


FIG. 38. — *Zoosphaerium blandum* (de Saussure & Zehntner, 1902): **A-H** holotype; **A**, coxa of 1st left leg with 1st stigma-carrying plate, posterior view; **B**, 9th left leg; **C**, coxa of 2nd left leg with gonopore; **D-F** left anterior telopod; **D**, anterior view; **E**, posterior view; **F**, joints 2-4, inner view; **G, H**, left posterior telopod, joints 2 and 3; **G**, anterior view; **H**, posterior view; **I**, joints 2 and 3 of right posterior telopod, anterior view (MNHN CB011); **J**, joints 2 and 3 of right posterior telopod, anterior view (FMMC 5372). Abbreviations: **Cx**, coxa; **St**, stigma-carrying plate. Scale bars: 1 mm.

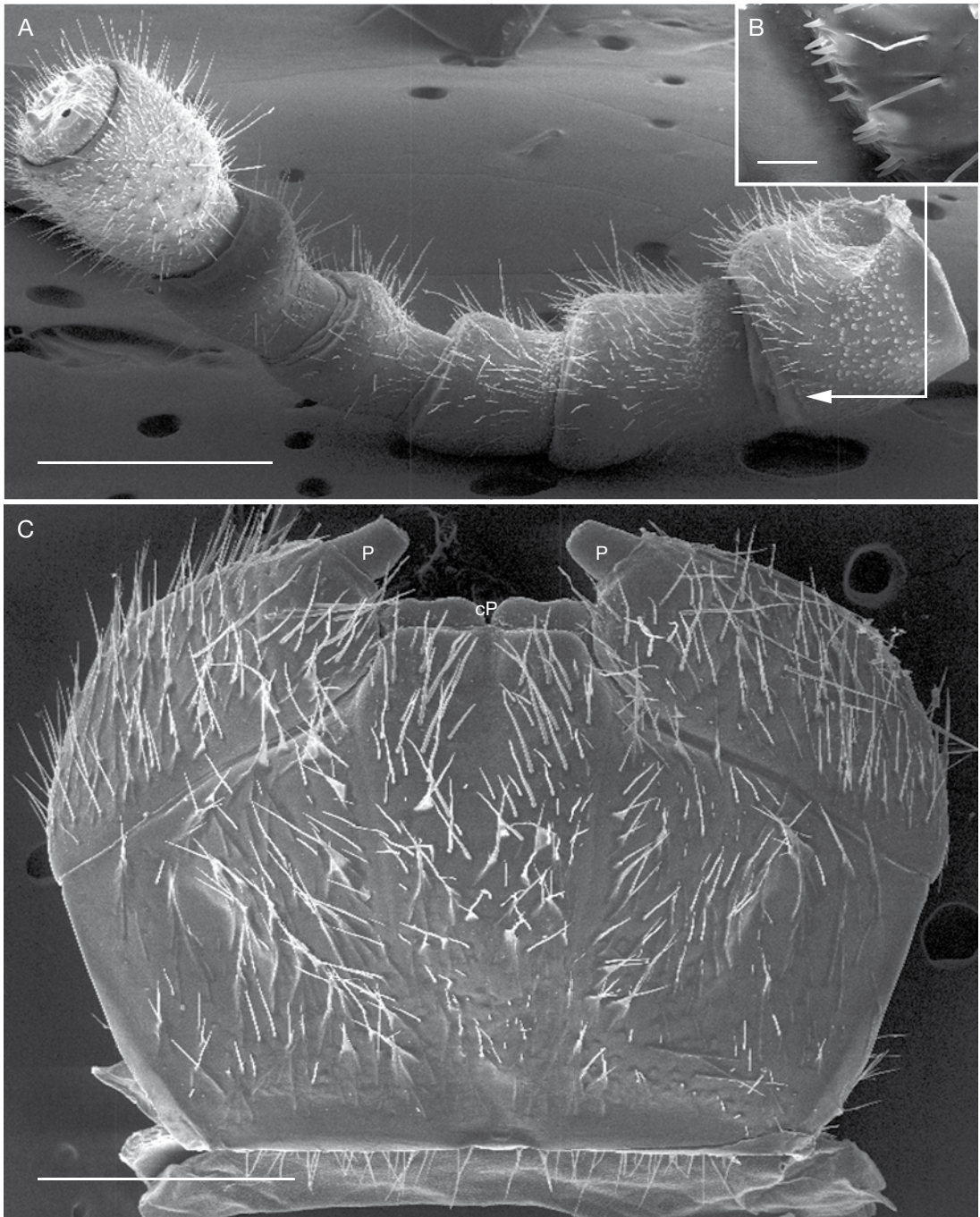


FIG. 39. — *Zoosphaerium blandum* (de Saussure & Zehntner, 1902), SEM (FMMC 5372): **A**, **B**, right antenna; **A**, overview, lateral view; **B**, sensory (?) cones on first joint; **C**, gnathochilarium, anterior side. Abbreviations: **cP**, central pads; **P**, palpus. Scale bars: **A**, 1 mm; **B**, 40 µm; **C**, 800 µm.

Mandible: with 6 rows of pectinate lamellae; number of teeth decreasing proximad (Fig. 40B). Condylus with 2 strongly developed steps at apical and inner margin, both steps of same strength (Fig. 40B).

Gnathochilarium: ventral side with some bristles (Fig. 39C). No sensory cones detectable lateral of palpi (Figs 40A). Sensory uvulae on central pads not clearly visible (Fig. 40A).

Collum: all hairs standing in pits. Anterior margin with *c.* 25 long hairs, posterior margin with only *c.* 16 long hairs. Remaining part of collum glabrous.

Thoracic shield: surface similar to those of tergites. Extensions shallow.

Tergites: tips of posterior paratergite margins not (!) projecting posteriorly. Tergites smooth and glabrous, at high magnification ($> 40\times$) a weak leather-like surface becomes visible.

Endotergum: internal section with numerous slim, long spines and bristles (Fig. 45A). Two rows of cuticular patterns, anteriorly large grooves, separated from one another, posteriorly small circular spots in touch with the ridge, located close to one another (Fig. 45A). Externally a single row of marginal bristles. Bristles long, surmounting posterior end of tergite (Fig. 45A).

Anal shield: weakly rounded, not bell-shaped but weakly tapered with steeper slope. Reaching its hindmost point on a small process of its lower side. In contrast to smooth tergites covered with numerous small hairs. Hairs located only on slope, especially toward its hindmost end. Underside carrying a variable number of locking carinae (see intraspecific variation). A distinct suture between both carinae, representing border of 13th tergite fused to anal shield.

Legs: first tarsi with 2-4, second with 3-5 long ventral spines. First 2 tarsi with only weakly curved claws and without apical spine. Tarsi 3-21 with curved claws, 8-12 ventral spines and an apical spine (Fig. 38B). Femur 1.6 times, tarsi 3.5 times longer than wide. Femora with crenulated ridge (Fig. 38B).

Stigma-carrying plate: first stigma-carrying plate lobe long, surmounting coxa 1. Plate covered sparsely with hairs, particularly around apical margin. Lobe

almost straight, only weakly curved towards coxa, ending broad and blunt (Fig. 38A).

Female unknown.

Male sexual characters: male gonopore small, covered with single, large, sclerotized, undivided and rounded plate. Apical part of plate membranous. Gonopore covering 1/3 of height and 1/2 of coxal width (Fig. 38C). Anal shield well-rounded, covered with field of small hairs around hindmost point.

Anterior telopods: first joint with a stridulation harp and 2 stridulation ribs. Both ribs straight, lateral one much longer and better developed than internal rib (Fig. 38D). Second joint on posterior side with lobe like, weakly curved process with rounded edges (Fig. 38E, F). Point of process protruding up to half of third joint height, towards third joint with sclerotized spots (Fig. 38F). Apical margin of third joint well-rounded. Third joint with a cavity juxtaposed to second joint. Internal margin towards cavity with numerous sclerotized spots and a single small spine located closely towards tip. One additional short spine arising inside of cavity juxtaposed to second joints process (Fig. 38E, F). Syncoxite on both sides without hair (Fig. 38D). Only lateral borders of first joint sparsely covered with hair.

Posterior telopods: third joint curved and especially at inner margin irregularly rounded. Hollowed-out margin towards second joint with single large lobe and up to five smaller, sclerotized spines (Fig. 38G, I, J). Third joint on posterior aspect with one row of *c.* 16 crenulated teeth (Fig. 38H). Process of second joint as wide as third joint, with strongly arched tip. Anterior side basally with single membranous lobe and sclerotized spine (can be absent in some specimens), furthermore on whole inner margin around the tip with small, sclerotized spots juxtaposed to third joint. Second and third covered on both sides with long hairs, tips of both only laterally with isolated hairs (Figs 38G-J). Inner horns broad, with pointed tip arched backwards and covered with small hairs.

INTRASPECIFIC VARIATION

The 5 male specimens differ a lot in some characters, which seem to be stable in other giant pill-millipede species (Wesener & Sierwald 2005a). Even specimens from the same locality (the types of

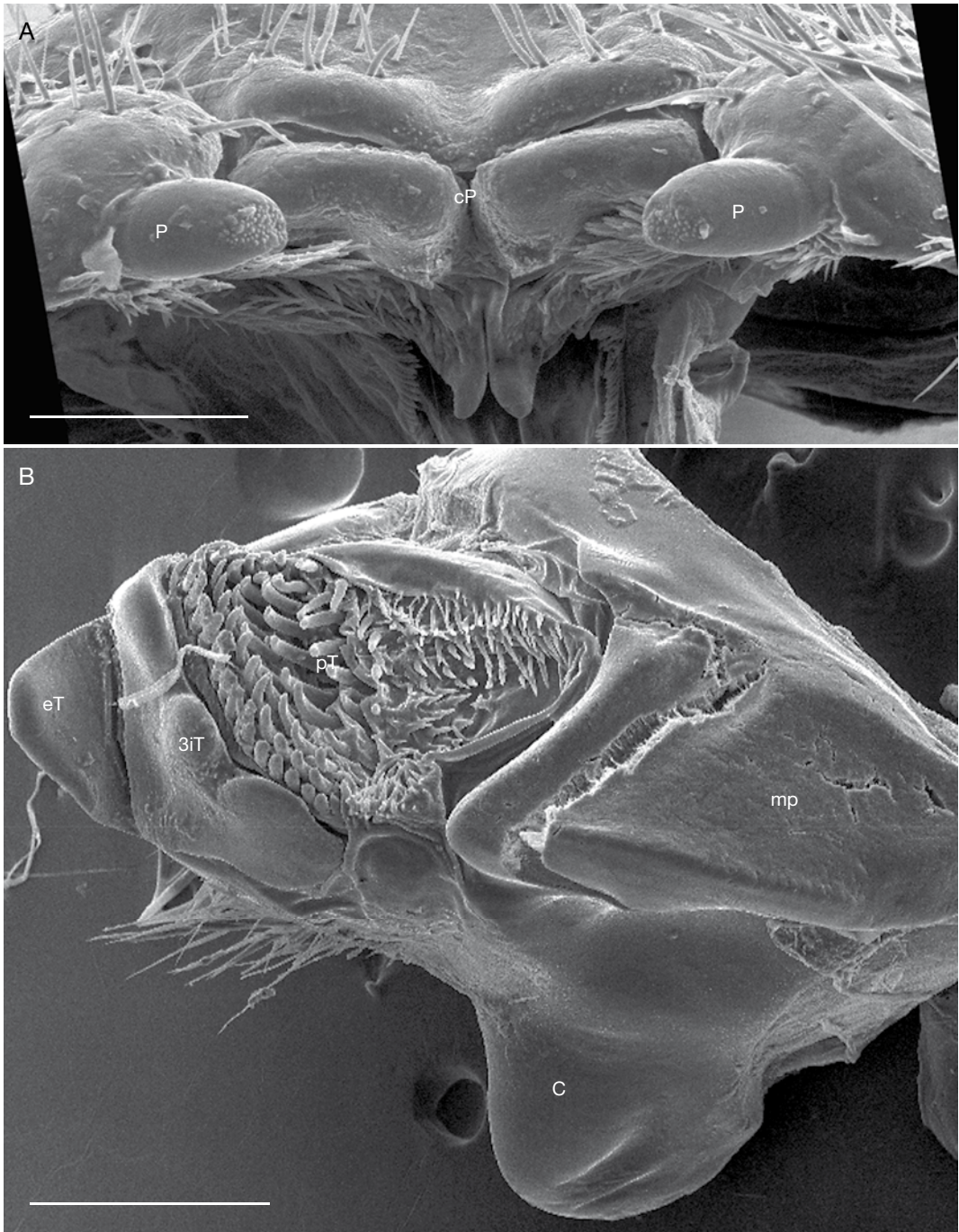


FIG. 40. — *Zoosphaerium blandum* (de Saussure & Zehntner, 1902), SEM (FMMC 5372): **A**, gnathochilarium, apical view; **B**, mandible, overview. Abbreviations: **3iT**, 3 internal teeth; **C**, condylus; **cP**, central pads; **eT**, external tooth; **mp**, molar plate; **P**, palpus; **pT**, pectinate lamella. Scale bars: A, 300 μ m; B, 500 μ m.

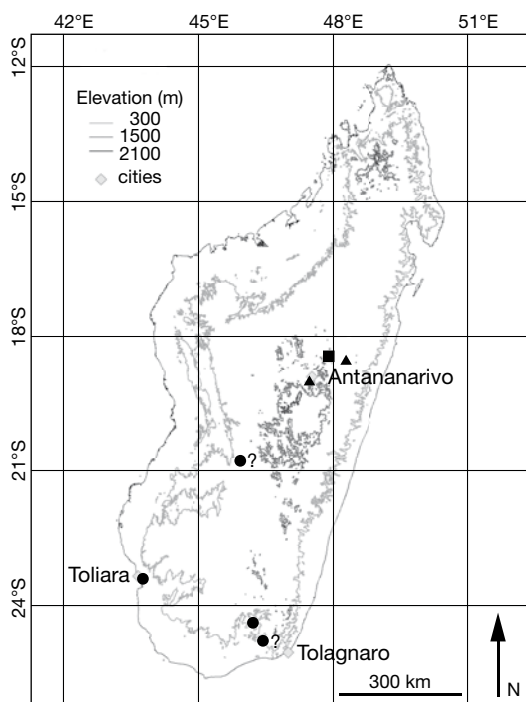


FIG. 41. — Distribution map of *Zoosphaerium platylabum* (de Saussure & Zehntner, 1897) (▲), *Z. blandum* (de Saussure & Zehntner, 1902) (●) and *Z. piligerum* (de Saussure & Zehntner, 1897) (■).

Z. blandum and *Z. stridulator*) show variation in the development of the closing ledges on the anal shield. Some specimens show no carinae, others just 1, the specimen from Andohahela, 1 weak and 1 small dot-like posterior carina, and the type of *Z. stridulator* has 1 small and 1 long closing carinae. There is also variation in the number of spines and lobes on the chelae of posterior telopods. More material is necessary to evaluate the intraspecific variation of this species. Possibly genetic studies may show if *Z. blandum* includes cryptic species, or if the large amount of intraspecific variation is the effect of a hybridization process.

DISTRIBUTION AND ECOLOGY

This species shows a distribution around the dry forest in the southern part of Madagascar (Fig. 41). In two of four localities it was found together with *Z. libidinosum*.

CONSERVATION

Because of the wide distribution in one of the least anthropogenically-affected Malagasy ecoregions (Fig. 41), this species seems not to be under a threat of extinction.

REMARKS

In the original description of *Sphaerotherium stridulator*, de Saussure & Zehntner (1902) already mentioned that this species is closely related to *Z. blandum*, which has even the same type locality. Observation of the type material at the MNHN revealed that the original description by de Saussure & Zehntner (1902) had one eminent mistake: the drawing of anterior telopods shows and also the description text states that *S. stridulator* has 3 stridulation ribs, which would be a unique feature in the genus *Zoosphaerium*. Nevertheless, the studied holotype of *S. stridulator* has just 2 stridulation ribs, without any trace of a third one. Also the general appearance, shape of anal shield and number of sensory cones on the antennae, is the same in both type specimens. With these facts it is proposed to synonymize *Sphaerotherium stridulator* de Saussure & Zehntner, 1902 with *Zoosphaerium blandum* (de Saussure & Zehntner, 1897).

Species only known from females or immature males

The following species are only known from females or immature males, nevertheless, precise type localities and unique characters for Malagasy Sphaerotheriida allow the identification of these species. For a placement into species-groups, more material of these species, particularly mature males, would be necessary.

Zoosphaerium sakanum (Attems, 1910) (Fig. 42)

Sphaerotherium sakanum Attems, 1910: 85, fig. 1, pl. 10, figs 1-4.

Zoosphaerium sakanum – Jeekel 1999: 12 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — Leg. Voeltzkow, 2 ♂♂ (immature, 1 broken and without telopods), 2 ♀♀ (immature) syntypes (ZMB 5038).

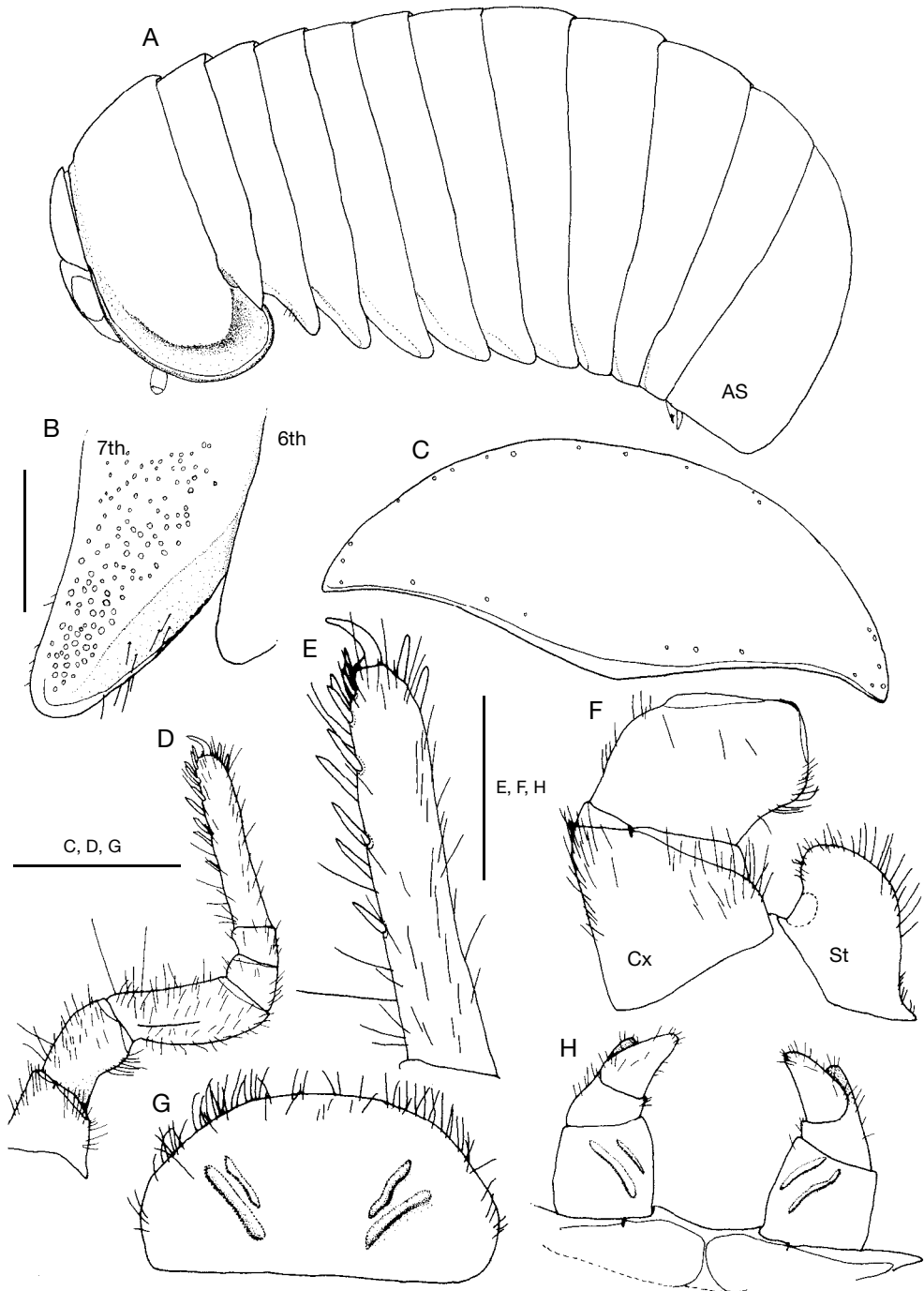


FIG. 42. — *Zoosphaerium sakanum* (Attems, 1910), paratype: **A**, habitus, body length 24.4 mm; **B**, 7th paratergite; **C**, collum, 1st tergite; **D**, 9th left leg; **E**, tarsus of 9th left leg; **F**, coxa and prefemur of 1st right leg with 1st stigma-carrying plate; **G**, female subanal plate; **H**, anterior telopods, anterior view. Abbreviations: **AS**, anal shield; **Cx**, coxa; **St**, stigma-carrying plate. Scale bars: B-H, 1 mm.

TYPE LOCALITY. — Madagascar, Sakana (East Madagascar), “Urwald” (probably: province Toamasina, 17°18'0"S, 49°1'60"E).

DIAGNOSIS. — Only immature material available. Individuals up to 24.5 mm long, body high and compressed. Tips of paratergites not projecting posteriorly (Fig. 42A). Tergites covered with numerous small, circular pits (Fig. 42B). Sixth antennomere with 11-18 sensory cones. Anterior telopods with 2 (Fig. 42H), female washboard with 2 up to 3 stridulation ribs (Fig. 42G).

SIMILAR SPECIES

Because all individuals are immature, no comparison with other species could be made.

DESCRIPTION

Body measurements: immature males (2 specimens): length 17.45, width of thoracic shield 8.55, height of thoracic shield 5.25. Immature females (2 specimens): length up to 24.4, width up to 10.5, height up to 6.35.

Habitus: body high and compressed (Fig. 42A). Tergites glabrous but covered with numerous small, rounded pits (Fig. 42B).

Coloration: white, completely faded, only eyes green.

Head: posterior margin of head towards collum without hair.

Antennae: sixth joint of cylindrical shape with 11-18 sensory cones. First joint short but remarkably broader than others. At least first joint with sclerotized teeth. Mouthparts not dissected.

Collum: anterior margin with 9, posterior margin with 17 small (hair-?) pits. Remaining part of collum glabrous (Fig. 42C).

Thoracic shield: surface like tergites covered with numerous small pits (Fig. 42A, B).

Tergites: tips of paratergite posterior margins straight, not projecting posteriorly. Tergites without hair, but completely covered with small, circular pits (Fig. 42B).

Endotergum: internal section with short spines and isolated bristles (Fig. 45B). One row of circular cuticular patterns, distance between the patterns larger than their diameter (Fig. 45B). Externally a single row of marginal bristles. Bristles protruding up to 1/3 towards posterior tergite margin (Fig. 45B).

Anal shield: well-rounded (Fig. 42A), like tergites covered with small, circular pits. Underside carries two well-developed black locking carinae on both sides, anterior one small, but well-developed, posterior carina 3 times longer than first. Locking carinae separated from each other by a distance equal to half of shorter carina length.

Legs: tarsi 3-21 with curved claws, *c.* 9 ventral spines and an apical spine (Fig. 42E). Ninth femur 2.1 times longer than wide, tarsi 5.3 times longer than wide (Fig. 42E). Femora with crenulated ridge of medium length (Fig. 42D).

Stigma-carrying plate: first stigma-carrying plate lobe short and stout, protruding up to apical edge of coxa 1. Lobe apically covered with isolated, long hairs, weakly curved towards coxa, on broad, stout tip only slightly thinner than more basally (Fig. 42F).

Female sexual characters: female immature. Subanal plate on each side with 2 short, but straight and well-developed stridulation ribs (Fig. 42G). Vulva small (immature specimens). Operculum notched (see Attems 1910: fig. 1 for a detailed drawing).

Male sexual characters: male gonopore minute, almost invisible. Anal shield shaped like in female specimens.

Anterior telopods: with 2 stridulation ribs. Rest of telopods immature (Fig. 42H).

Posterior telopods: unusual shape, because specimens are immature (see Attems 1910: pl. 10, fig. 1: 3-4).

INTRASPECIFIC VARIATION

The drawings of anterior telopods in the original descriptions are incorrect, they show only a single stridulation rib. Some legs have two apical spines on the tarsus (Fig. 42E).

DISTRIBUTION AND ECOLOGY

This species is until now only known from the rainforest at Sakana.

CONSERVATION

Field studies and collections are necessary to evaluate if *Z. sakanum* still exists.

Zoosphaerium fraternarium Jeekel, 1999
(Fig. 43)

Sphaerotherium fraternum de Saussure & Zehntner, 1897: pl. 5, fig. 10; 1902: 50. Not *Sphaerotherium fraternum* Butler, 1872 from Victoria, Australia.

Zoosphaerium fraternarium Jeekel, 1999: 12 nom. nov. — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — Leg. M. Catat, 1890, ♀ holotype (MNHN CB024).

TYPE LOCALITY. — Madagascar.

OTHER MATERIAL EXAMINED. — **Madagascar.** Province Fianarantsoa, forêt de l’Kongo (= Fort-Carnot), leg. G. Grandidier, 1899, 1 ♀ (MNHN n° 31).

DIAGNOSIS. — Individuals up to 37 mm long, body high (Fig. 43A). Tips of paratergites projecting posteriorly (Fig. 43A). Tergites glabrous, at high magnification an orange-like surface becomes visible. Sixth antennomere with 12 or 13 sensory cones. Female washboard on each side with 2 stridulation ribs. Vulva large, internal plate and operculum surmounting coxa (Fig. 43E). Operculum unique, anterior margin deeply notched, with 2 well-developed separated lobes. Lobes rounded, of same size, inner lobe protruding slightly higher than lateral lobe (Fig. 43E). Anal shield well-rounded, slightly tapered (Fig. 43A), inner side with two well-developed black locking carinae (Fig. 43C). Endotergum with 2 or 3 rows of extraordinary long marginal bristles (Fig. 47C). Male unknown.

SIMILAR SPECIES

The shape of operculum is unique for Malagasy Sphaerotheriida. The only species with endotergum marginal bristles as long as those of *Z. fraternarium* is *Z. libidinosum*. From the latter species *Z. fraternarium* differs in characters on the anal shield, locking carinae and operculum.

DESCRIPTION

Body measurements: female (holotype): length 37.45, width of thoracic shield 19.4, height of thoracic shield 10.25.

Habitus: body high (Fig. 43A). Tergites without hair but at high magnification an orange-like surface becomes visible.

Coloration: brown, towards posterior margin of tergites laterally with darker brown pattern. Collum, head, antennae and tips of legs olive-green.

Head: posterior margin of head towards collum without hairs.

Antennae: sixth joint of cylindrical shape with 11 or 12 sensory cones. First joint short but remarkably broader than others. At least first joint with sclerotized teeth.

Mouthparts not dissected.

Collum: anterior and posterior margin with few, isolated hairs. Remaining part of collum glabrous.

Thoracic shield: surface structured like those of tergites (Fig. 43A).

Tergites: tips of paratergite posterior margin projecting posteriorly (Fig. 43A). Tergites without hair and with orange-like surface.

Endotergum: internal section with short spines and isolated bristles (Fig. 45C). Area damaged between marginal ridge and internal part. Externally 2 or 3 rows of marginal bristles, placed closely to one another. Bristles very long, surmounting posterior tergite margin (Fig. 45C).

Anal shield: well-rounded, like tergites with orange-like surface, covered with minute, isolated hairs. Shield reaching its hindmost point slightly above its lower side (Fig. 43A). Posterior end of lower side slightly tapered (Fig. 43A). Underside carrying 2 well-developed black locking carinae on both sides, anterior one small, but well-developed, posterior carina 4 times longer than first (Fig. 43C). Locking carinae separated from each other by a distance equal to shorter carina length (Fig. 43C).

Legs: first and second tarsi with four ventral spines, weakly curved claws and without apical spine, third tarsi with 7 ventral spines. Tarsi 3–21 with small curved claws, 8–10 ventral spines and an apical spine (Fig. 43D). Ninth femur 1.9 times longer than wide, tarsi 3.9 times longer than wide. Femora with short crenulated ridge (Fig. 43D).

Stigma-carrying plate: first stigma-carrying plate lobe short, but surmounting coxa 1. Lobe curved towards coxa, tip broad and stout, thinner than the more basal part (Fig. 43B).

Female sexual characters: subanal plate with a washboard, consisting of well-developed stridulation ribs, two ribs on each side. Vulva large, covering more than 4/5 of coxa (Fig. 43E). Operculum surmounting coxa, deeply notched, with two rounded lateral tips. Inner tip protruding

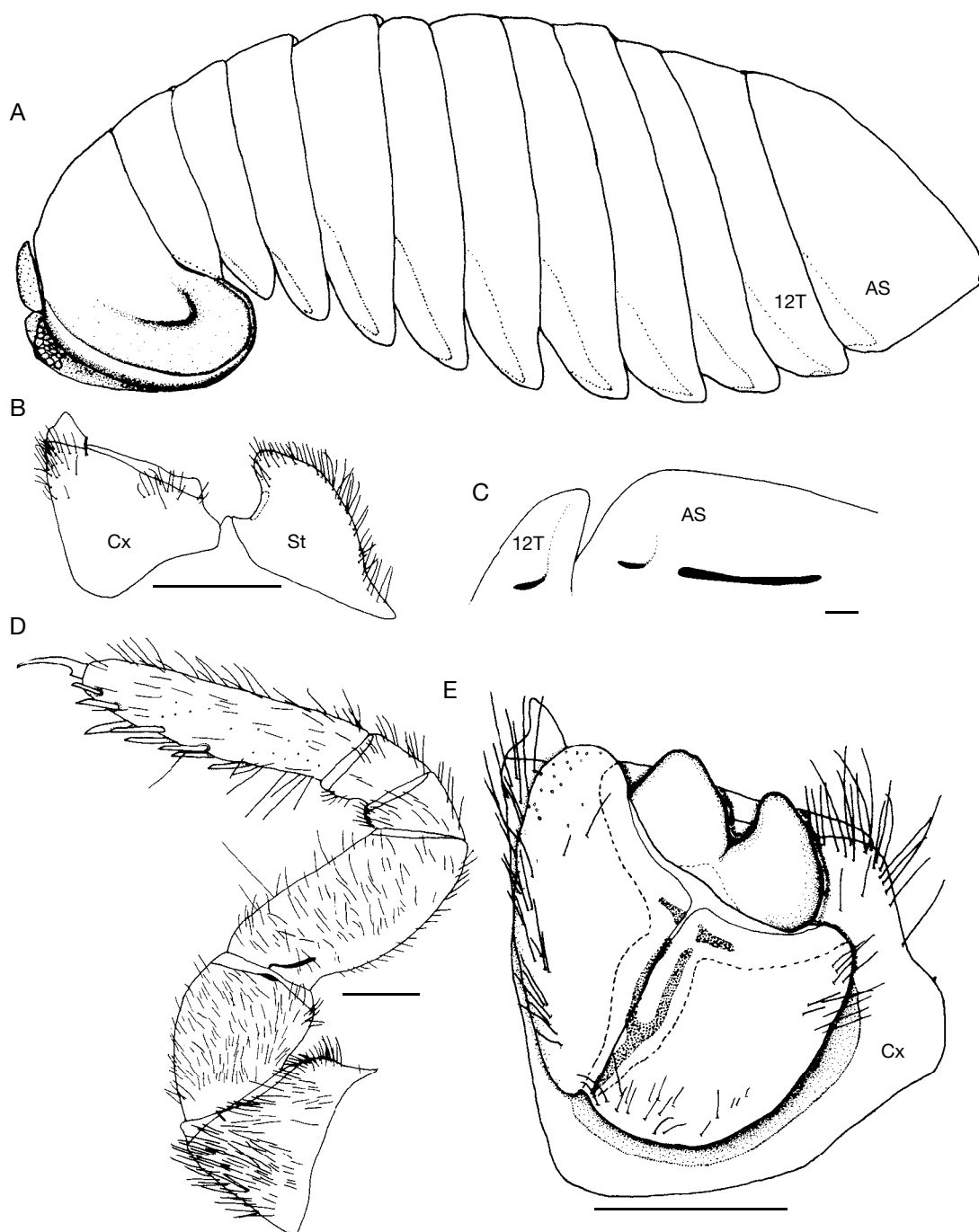


FIG. 43. — *Zoosphaerium fraternarium* Jeekel, 1999, holotype: **A**, habitus, body length 37.4 mm; **B**, coxa of 1st left leg with 1st stigma-carrying plate; **C**, closing ledges of anal shield; **D**, 9th left leg; **E**, coxa of 2nd left leg with vulva. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **St**, stigma-carrying plate. Scale bars: B-E, 1 mm.

slightly higher than lateral tip (Fig. 43E). Inner plate long, surmounting coxa, almost as high as operculum (Fig. 43E).

Male unknown.

DISTRIBUTION AND ECOLOGY

This species is still only known from the first description, giving no precise locality.

CONSERVATION

The conservation status of this species is completely unknown.

Zoosphaerium immane (Karsch, 1881) (Fig. 44)

Sphaerotherium immane Karsch, 1881: 30, pl. 2, fig. 1. — de Saussure & Zehntner 1897: pl. 5, fig. 13; 1902: 48.

Zoosphaerium immane — Jeekel 1999: 11 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — Leg. Dr H. Dorn, 2 ♀♀ syntypes (ZMB 715).

TYPE LOCALITY. — Madagascar.

DIAGNOSIS. — Individuals up to 58 mm long, body high. Tips of paratergites projecting slightly posteriorly (Fig. 44A). Tergites glabrous, at high magnification small pits become visible. Sixth antennomere with 4 sensory cones. Female washboard on each side with 2 or 3 discontinuous stridulation ribs (Fig. 44E). Vulva large, internal plate and operculum not surmounting coxa. Operculum medially weakly notched, with 2 lobes. Lobes rounded, lateral lobe protruding slightly higher than inner lobe (Fig. 44D). Anal shield well-rounded, inner side with 2 well-developed black locking carinae. Endotergum with 2 rows of marginal bristles (Fig. 45D). Male unknown.

SIMILAR SPECIES

Zoosphaerium immane has following unique combinations of characters: body length above 55 mm, antenna with 4 sensory cones, vulva not surmounting coxa.

DESCRIPTION

Body measurements: female (2 specimens): length up to 57.95, width of thoracic shield up to 31.1, height of thoracic shield up to 16.7.

Habitus: body high, with prominent thoracic shield (Fig. 44A). Tergites without hair but at high magnification small impressions become visible.

Coloration: brown, towards posterior margin of tergites with darker brown pattern. Collum, head, antennae and tips of legs also brown.

Head: posterior margin of head towards collum without hair. Eyes with 66–74 ocelli each.

Antennae: sixth joint of cylindrical shape with 4 sensory cones. First joint remarkably broader than others, but short, with single groove and sclerotized teeth.

Mouthparts not dissected.

Collum: anterior and posterior margin only laterally with few, isolated hairs. Remaining part of collum hairless.

Thoracic shield: surface similar to tergites (Fig. 44A).

Tergites: tips of paratergite posterior margins projecting slightly posteriorly (Fig. 44A). Tergites without hair and with small pits.

Endotergum: internal section with short spines and isolated bristles (Fig. 45D). One row of elliptical grooves, towards marginal ridge a second row of circle-like, deeper patterns (Fig. 45D). Externally 2 rows of marginal bristles, placed close to one another. Bristles long, reaching almost up to posterior tergite margin (Fig. 45D).

Anal shield: well-rounded, like tergites with small impressions (Fig. 44A). Underside carries 2 well-developed black locking carinae on both sides

Legs: first and second tarsi with 5 ventral spines, weakly curved claws and without apical spine, third tarsi with 7 ventral spines. Tarsi 3–21 with small curved claws, 8–10 ventral spines and an apical spine. Ninth femur 1.9 times longer than wide, tarsi 5.4 times longer than wide. Femora with crenulated ridge of medium length (Fig. 44C).

Stigma-carrying plate: first stigma-carrying plate lobe short, not surmounting coxa. Lobe only weakly curved towards coxa. Broad, stout tip slimmer than basal part (Fig. 44B).

Female sexual characters: subanal plate with a washboard, consisting of irregular, sometimes non-continuous, short stridulation ribs, 3 ribs on each side (Fig. 44E). Vulva large, covering more than

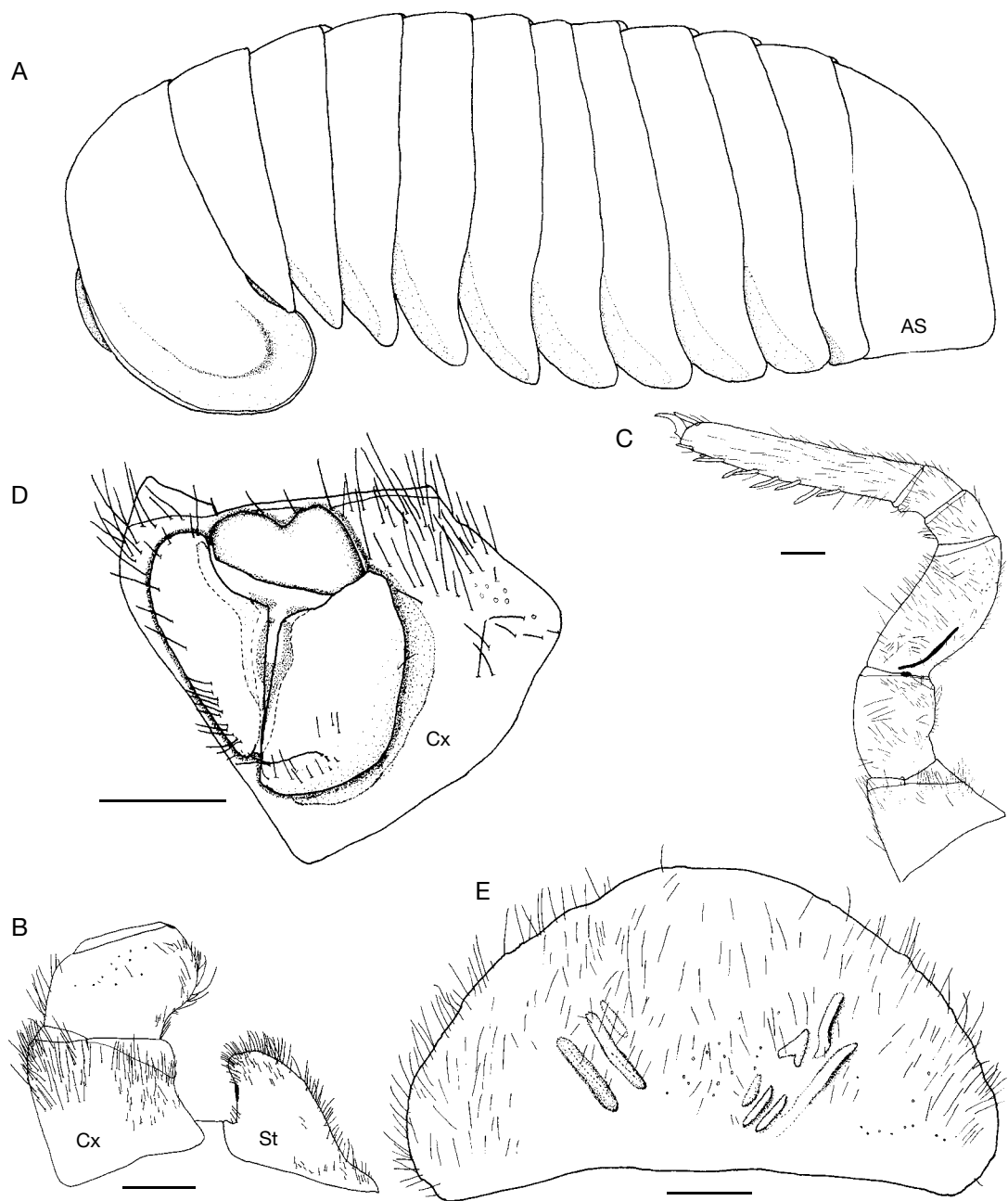


FIG. 44. — *Zoosphaerium immane* (Karsch, 1880), lectotype: **A**, habitus, body length 58 mm; **B**, coxa of 1st left leg with 1st stigma-carrying plate; **C**, 9th left leg; **D**, coxa of 2nd left leg with vulva; **E**, subanal plate. Abbreviations: **AS**, anal shield; **Cx**, coxa; **St**, stigma-carrying plate. Scale bars: B-E, 1 mm.

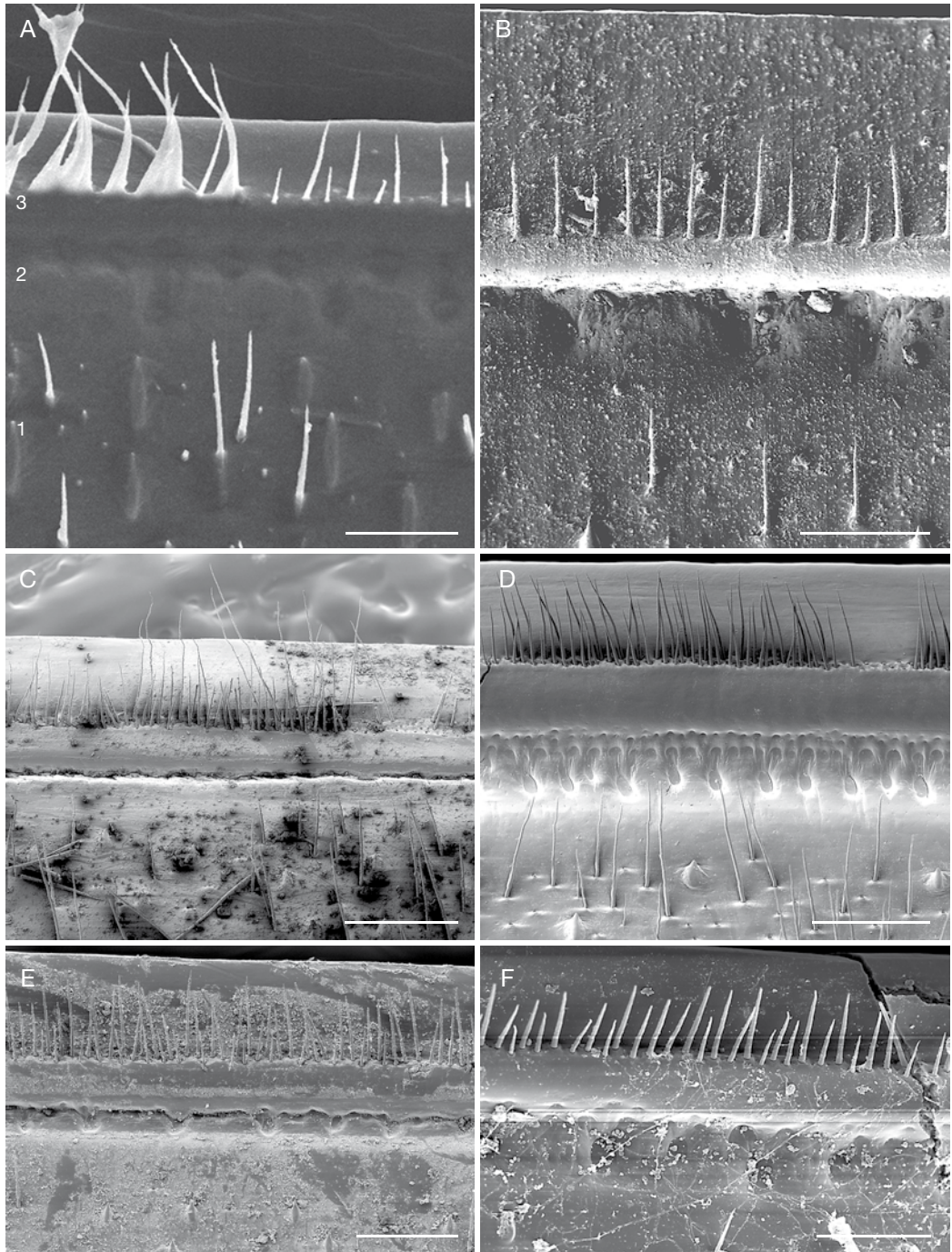


FIG. 45. — Endoterga of midbody tergites, SEM: **A**, *Zoosphaerium blandum* (de Saussure & Zehntner, 1902) (FMMC 5372); **B**, *Z. sakanum* (Attems, 1910), paratype; **C**, *Z. fraternarium* (Jeekel, 1999), holotype; **D**, *Z. immane* (Karsch, 1880), lectotype; **E**, *Z. anale* (de Saussure & Zehntner, 1897), holotype; **F**, *Z. ? reticulatum* (Butler, 1878), lectotype. Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section. Scale bars; A, B, 100 µm; C, D, 300 µm; E, 200 µm; F, 90 µm.

2/3 of coxa (Fig. 44D). Operculum low, not surmounting coxa. Apical margin of operculum only weakly notched, with 2 rounded tips. Lateral tip protruding slightly higher than inner tip (Fig. 44D). Inner plate long, protruding as high as basal half of operculum (Fig. 44D).

Male unknown.

DISTRIBUTION AND ECOLOGY

This species is until now only known from the first description, giving no precise locality.

CONSERVATION

The conservation status of this species is completely unknown.

Zoosphaerium anale

(de Saussure & Zehntner, 1897)

(Fig. 46)

Sphaerotherium anale de Saussure & Zehntner, 1897: pl. 4, fig. 4; 1902: 30.

Zoosphaerium anale – Jeekel 1999: 9 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — Leg. A. Grandidier, ♀ lectotype (here designated) (MNHN CB007).

TYPE LOCALITY. — Madagascar, south-west coast.

DIAGNOSIS. — Individuals up to 53 mm long, body high. Tips of paratergites slightly projecting posteriorly (Fig. 46A). Tergites glabrous, at high magnification small, dot-like impressions become visible. Sixth antennomere with 22 sensory cones. Female washboard on each side with 2, short, sometimes discontinuous, stridulation ribs. Vulva large, internal plate and operculum slightly surmounting coxa. Operculum medially notched and with 2 lobes. Lobes of the same size, rounded (Fig. 46D). Anal shield weakly bell-shaped and tapered (Fig. 46A), covered with some small hairs, inner side with 2 well-developed black locking carinae (Fig. 46C). Endotergum with 2 rows of marginal bristles (Fig. 45E). Male unknown.

SIMILAR SPECIES

Zoosphaerium anale has the following unique combinations of characters: body length up to 53 mm, antenna with 22 sensory cones, vulva slightly surmounting coxa with 2 well-rounded, same-sized

lobes, tip of first stigma-carrying plate pointed, 1 short and 1 longer locking carina on anal shield, anal shield weakly bell-shaped and tapered.

DESCRIPTION

Body measurements: female (lectotype): length 29.9 (in first description: 53.0), width of thoracic shield 15.5 (in first description 26.5), height of thoracic shield 9.15.

Habitus: body high, with prominent thoracic shield (Fig. 46A). Tergites without hair but at high magnification small, dot-like pits become visible.

Coloration: faded, brown, head, antennae and tips of legs with traces of green.

Head: posterior margin of head towards collum without hairs.

Antennae: sixth joint of cylindrical shape, with 22 sensory cones. First joint remarkably broader than others, but short and with sclerotized teeth.

Mouthparts not dissected.

Collum: anterior and posterior margin with few, isolated hairs. Remaining part of collum also with some isolated hairs.

Thoracic shield: surface similar to tergites (Fig. 46A).

Tergites: tips of paratergite posterior margins projecting slightly posteriorly (Fig. 46A). Tergites glabrous, with small dot-like pits.

Endotergum: internal section with short spines and isolated bristles (Fig. 45E). One row of elliptical, almost circle-like deep patterns between marginal ridge and internal area. Those grooves isolated, standing in a far, regular distance from one another (Fig. 45E). External 2 rows of marginal bristles, placed close to one another. Bristles protruding 1/2-2/3 towards posterior tergite margin (Fig. 45E).

Anal shield: weakly bell-shaped, hindmost end tapered, covered with some small, isolated hairs (Fig. 46A). Underside carrying 2 well-developed black locking carinae on both sides, anterior one small, but well-developed, posterior carina 3.5 times longer than first (Fig. 46C). Locking carinae separated from one another by a distance equal to shorter carina length. A distinct suture between both carinae, representing border of 13th tergite fused to anal shield (Fig. 46C).

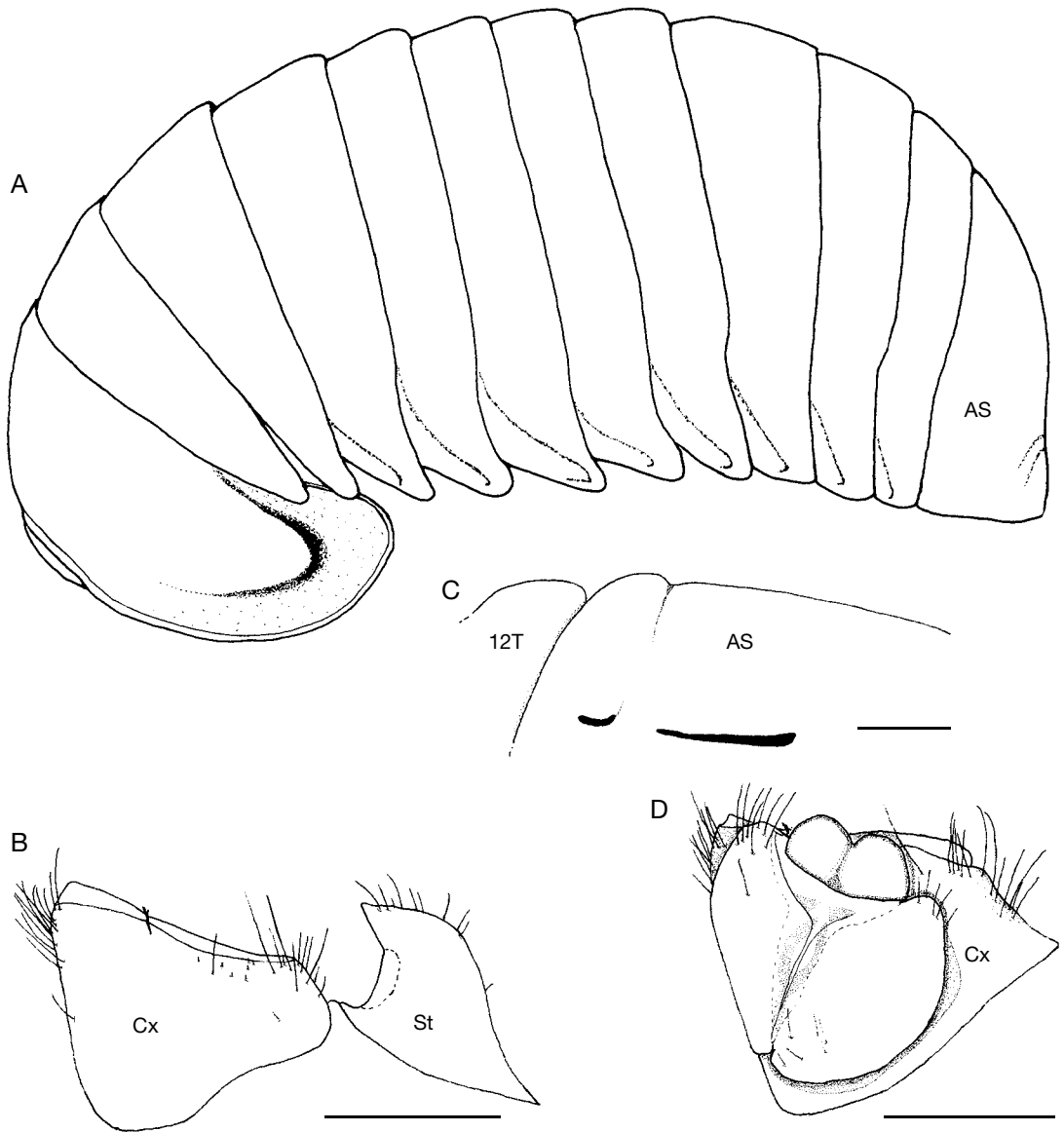


FIG. 46. — *Zoosphaerium anale* (de Saussure & Zehntner, 1897), holotype: **A**, habitus, body length 30 mm; **B**, coxa of 1st left leg with 1st stigma-carrying plate; **C**, closing ledges of anal shield; **D**, coxa of 2nd left leg with vulva. Abbreviations: **12T**, 12th tergite; **AS**, anal shield; **Cx**, coxa; **St**, stigma-carrying plate. Scale bars: B-D, 1 mm.

Legs: first tarsi with 4, second tarsi with 5 ventral spines, weakly curved claws and without apical spine. Tarsi 3-21 with small curved claws and an apical spine.

Stigma-carrying plate: first stigma-carrying plate lobe long, surmounting coxa. Lobe strongly curved

towards coxa, with sharp, pointed tip (Fig. 46B).

Female sexual characters: subanal plate with a washboard, consisting of irregular, sometimes discontinuous, short stridulation ribs, 2 ribs on each side. Vulva large, covering more than 2/3 of coxa (Fig. 46D). Operculum surmounting coxa, medially

notched, with two rounded lateral tips, both tips of same height (Fig. 46D). Inner plate long, also slightly surmounting apical margin of coxa, almost as high as basal half of operculum, exterior plate reaching around its base (Fig. 46D).

Male unknown.

DISTRIBUTION AND ECOLOGY

This species is until now only known from the first description, just stating “south-west coast”.

CONSERVATION

The conservation status of this species is completely unknown.

Zoosphaerium? *reticulatum* (Butler, 1878) (Fig. 47)

Sphaerotherium reticulatum Butler, 1878: 301. — de Saussure & Zehntner 1902: 68 (lists species name).

Zoosphaerium reticulatum – Jeekel 1999: 14 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — Two syntypes of unknown sex (second pair of legs and underside of anal shield missing) (BMNH).

TYPE LOCALITY. — Madagascar.

DIAGNOSIS. — Small individuals, with traces of green. Antenna with 20 sensory cones. Surface of tergites leather-like (Fig. 47A). Legs with weakly developed coxal lobe, furthermore inner margin of femur toothed (Fig. 47B). Anal shield well-rounded, with 2 locking carinae (Fig. 47D).

SIMILAR SPECIES

The toothed femur and the presence of a small coxal lobe separates *Z. reticulatum* from all other Malagasy Sphaerotheriida.

DESCRIPTION

Body length: small.

Coloration: faded, greenish-brown. Head, antennae and tips of legs brown.

Head: posterior margin of head towards collum without hair.

Antennae: sixth joint of cylindrical shape with 20 sensory cones.

Mouthparts not dissected.

Collum: unknown.

Thoracic shield: Concave lateral extensions broad and deep, with some isolated hairs. Marginal brim anteriorly thicker.

Tergites: anterior paratergite depressions of tergites 3-12 with isolated hairs. Paratergite tips projecting slightly posteriorly.

Endotergum: internal section with short spines and isolated bristles (Fig. 45F). One row of elliptical, deep grooves between marginal ridge and internal area. These grooves standing isolated in a regular distance from one another (Fig. 45F). External 2 rows of marginal bristles, placed close to, but not touching one another. Bristles short, reaching between marginal ridge and posterior tergite margin (Fig. 45F).

Anal shield: well-rounded, glabrous. Underside carrying two well-developed black locking carinae on both sides. Anterior carina small, but well-developed, posterior carina twice as long as first. Locking carinae separated from each other by a distance equal to half of shorter carina length (Fig. 47D).

Legs: tarsi 3-21 with small curved claws, 8 or 9 ventral spines and one apical spine. Ninth leg with small coxal lobe, femur 1.9 times longer than wide, tarsi 4.6 times longer than wide (Fig. 47B). Femora with crenulated ridge of medium length (Fig. 47B), furthermore inner margin of femur toothed (Fig. 47B).

Stigma-carrying plate: first stigma-carrying plate lobe surmounting coxa. Lobe weakly curved towards coxa, with well-rounded tip (Fig. 47C).

Female sexual characters: unknown.

Male sexual characters: unknown.

REMARKS

It is unclear whether the type specimens are adults. All characters which would allow a placement of this species in *Zoosphaerium* are absent. It remains unclear if this species represents a member of *Zoosphaerium*, furthermore, it remains possible, that *Z. reticulatum* is no Malagasy giant pill-millipede species. Nevertheless, the endotergum, femur pattern and other characters make an identification of this species possible, so that it is not listed under *nomina dubia*.

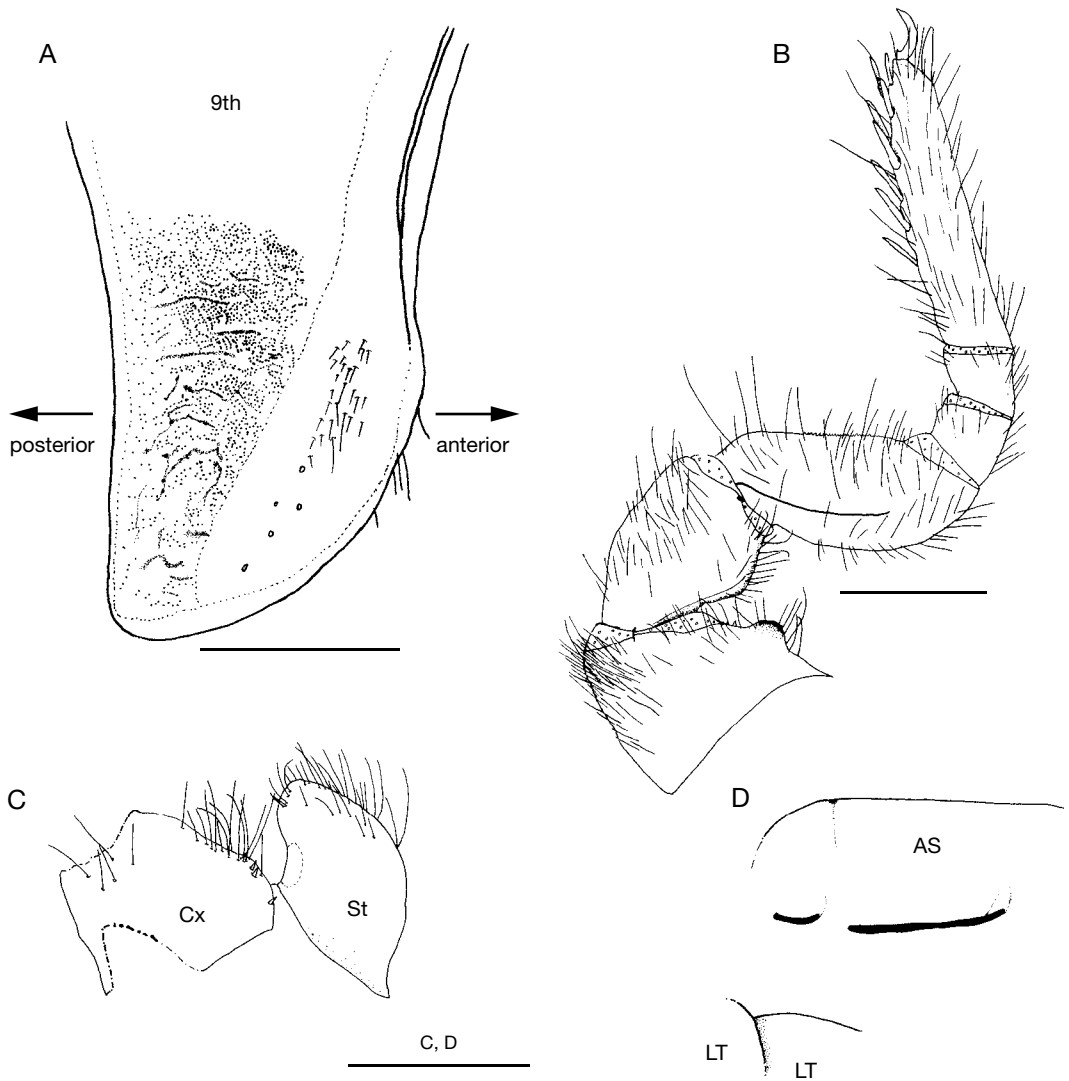


FIG. 47. — *Zoosphaerium?* *reticulatum* (Butler, 1878), lectotype: **A**, 9th paratergite, detail; **B**, 9th left leg; **C**, coxa of 1st left leg with 1st stigma-carrying plate; **D**, closing ledges of anal shield. Abbreviations: **AS**, anal shield; **Cx**, coxa; **LT**, laterotergite; **St**, stigma-carrying plate. Scale bars: A, 5 mm; B-D, 1 mm.

Sphaerotherium elongatum Brandt, 1833

Sphaerotherium insulanum Karsch, 1881: 30, pl. 2, fig. k, n. syn.

Zoosphaerium insulanum – Jeekel 1999: 14 (lists species name).

TYPE MATERIAL. — ♂ holotype (ZMB 570).

TYPE LOCALITY. — Mauritius.

REMARKS

A study of the endotergum shows clearly that *Zoosphaerium insulanum* represents a (possibly introduced) South African sphaerotheriid species of the genus *Sphaerotherium*. The genus *Zoosphaerium* is obviously strictly endemic to Madagascar. See Van den Spiegel *et al.* 2002 for a revision of this species.

NOMINA DUBIA

The types of the following species, are lost or damaged, a type locality is not given and the original descriptions are not suitable for a species determination.

Zoosphaerium actaeon (White, 1859)

Zephronia actaeon White, 1859: 405, pl. 7, figs 5-5b.

Sphaerotherium actaeon – de Saussure & Zehntner 1897: pl. 1, figs 1-1b, pl. 5, fig. 12 (redescription without viewing of holotype); 1902: 40, pl. 15, fig. 11 (redescription without viewing of holotype). — Brolemann 1922 (no description or drawing).

Zoosphaerium actaeon – Jeekel 1999: 10 (lists species name). — Enghoff 2003: 620 (lists species name).

MATERIAL EXAMINED. — **Madagascar.** Unknown locality, leg. Coquerel, det. H. de Saussure 1902, 1 ♀ (broken, premature) (MNHN CB001). — Nosy Bé, leg. Deyrolle, det. H. de Saussure 1902, 2 ♀♀ (damaged) (MNHN CB002). — Unknown locality, det. H. de Saussure, 1 ♀ (broken, with eggs) (MNHN CB003). — Côte est, leg. Lantz, 1882, det.?, 1 ♀ (broken into pieces) (MNHN CB004). — Unknown locality, coll. M. Lantz (Grandidier), 1903, det.?, 2 ♀♀ (dried, 1 immature) (MNHN CB005).

REMARKS

The holotype of *Z. actaeon* is no longer in the collections of the BMNH. The only characters given in the first description is the size, brown coloration and the fact that the surface has an orange-like pattern. The material de Saussure and Zehntner obviously used for their redescrptions includes at least three different species, one of them being *Zoosphaerium neptunus*, two others being undescribed. Because all specimens are females, always without precise locality and damaged, it is impossible to select a neotype. Recent collected material of the CAS and FMNH giving precise localities includes seven morphospecies of giant pill-millipedes with characters similar to those of *Z. actaeon*, unfortunately all of them only present the female sex. *Zoosphaerium actaeon* was considered synonym of *Sphaerotherium hippocastanum* by Butler (1873: 176).

Zoosphaerium hippocastanum (Gervais, 1847) (Fig. 48)

Sphaerotherium hippocastanum Gervais, 1847: 83. — Butler 1873: 176. — Lenz 1880: 153 (no drawing). — de Saussure & Zehntner 1897: pl. 5, fig. 15; 1902: 46. — Brolemann 1922: 230, figs 3-5.

Zoosphaerium hippocastanum – Jeekel 1999: 10 (lists species name). — Enghoff 2003: 620 (lists species name).

TYPE MATERIAL. — ♀ holotype (completely fragmented), (MNHN CB027).

TYPE LOCALITY. — Madagascar, Nosy Bé.

ADDITIONAL MATERIAL EXAMINED. — **Madagascar.** Nossi Bé (1627), leg. 1884, det. H. de Saussure 3 ♀♀ (one broken), (MNHN CB026). — Leg. Goudot, det. H. de Saussure, 1 ♀ (broken), (MNHN CB028). — Env. de Tanarive, coll. Acad. malgache, leg. Brolemann n° 2666, det. Brolemann, 3 ♂♂, 3 ♀♀ (MNHN CB029). — Env. de Tanarive, coll. Acad. malgache, leg. Brolemann n° 2666, det. Brolemann, 1 ♂ (MNHN CB030).

REMARKS

The 160-year old holotype of *Z. hippocastanum* is completely fragmented, the only visible characters are the locking carinae of the anal shield (Fig. 48B) and a groove with sclerotized teeth on the first joint of antenna. Even the endotergum is so strongly covered with irremovable dirt, that it contains only few informations (Fig. 48A). De Saussure & Zehntner (1902) were obviously the last and only persons, who reviewed the holotype. Nevertheless, the specimens determined by those authors as *Z. hippocastanum* and used for illustrations (MNHN CB026 and MNHN CB028) do include more than one species, the specimen used for illustrations represents in fact *Zoosphaerium neptunus*, from which *Z. hippocastanum* differs strongly in the shape of the locking carinae on the anal shield.

Then we have the material used for redescription by Brolemann (MNHN CB029 and CB030). This material is also not identical with the holotype of *Z. hippocastanum*, the locking carinae of the anal shield show a complete different position. It is not possible to select a better conserved neotype among the existing material. It may be possible to collect additional material from the island of Nosy Bé, if the type locality is really correct.

Zoosphaerium reflexum (Brolemann, 1922)

Sphaerotherium (*Globotharium*) *reflexum* Brolemann, 1922: 238, figs 14-17.

Zoosphaerium reflexum – Jeekel 1999: 13 (lists species name). — Enghoff 2003: 620 (lists species name).

REMARKS

The type of this species was stored by Brolemann at the Académie malgache, an institution that does no longer exist. Some of the material is now stored in the zoological collection at Tsimbazawa. It is unclear if the holotype and only known individual of *Z. reflexum* still exists in this collection. Even if it may exist, it is not available for loan. The original description was based on a female specimen, providing no unique characters. The original type locality is unknown. Brolemann (1922) stated that the individual was found in the collection of the Académie malgache.

Zoosphaerium elegans (Lenz, 1880)

Sphaerotherium elegans Lenz, 1880: 153. — de Saussure & Zehntner 1902: 48 (lists species name).

Zoosphaerium elegans – Jeekel 1999: 14 (lists species name). — Enghoff 2003: 620 (lists species name).

REMARKS

According to the original description, the male type specimen was in the possessions of the Senckenberg Institute. A search through the collection of the Senckenberg Museum by the first author did not lead to the rediscovery of the type. Furthermore, Lenz stated in a footnote that *Z. elegans* might represent the unknown male of *Z. hippocastanum*, because the individuals came from the same locality (Nosy Bé), and that Lenz wanted to synonymize them.

Zoosphaerium crassum (Butler, 1878)

Sphaerotherium crassum Butler, 1878: 301. — de Saussure & Zehntner: 68 (lists species name).

Zoosphaerium crassum – Jeekel 1999: 14 (lists species name). — Enghoff 2003: 620 (lists species name).

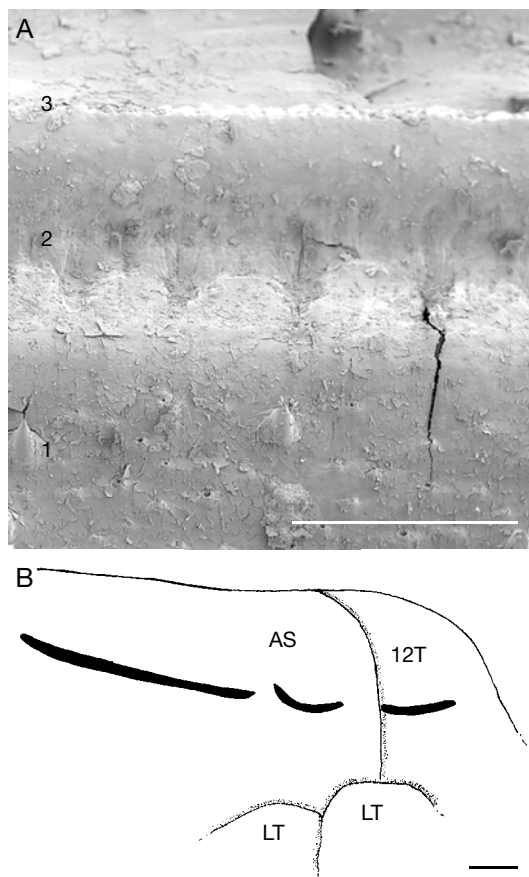


Fig. 48. — *Zoosphaerium hippocastanum* (Gervais, 1847), holotype: **A**, endotergum of midbody tergite; **B**, closing ledges of anal shield. Abbreviations: **1**, endotergum, internal section; **2**, endotergum, medial section; **3**, endotergum, external section; **12T**, 12th tergite; **AS**, anal shield; **LT**, laterotergite. Scale bars: A, 300 μ m; B, 1 mm.

REMARKS

The first description is not suitable for species identification, the precise type locality just stating Madagascar: Fianarantsoa. The only known type specimens seem no longer to exist.

Zoosphaerium stigmaticum (Butler, 1873)

Sphaerotherium stigmaticum Butler, 1873: 178, pl. 19, fig. 3. — de Saussure & Zehntner 1897: pl. 5, fig. 18 (reprint of Butler's figure); 1902: 67 (lists species name).

Zoosphaerium stigmaticum – Jeekel 1999: 14 (lists species name). — Enghoff 2003: 620 (lists species name).

REMARKS

According to the drawing by Butler (1873), the male of *Zoosphaerium stigmaticum* has a sclerotized knob on the hind face of the anal shield. Such a feature is not present in any single Malagasy giant pill-millipede species recorded so far. Although Butler states in the first description the type locality as Madagascar, it is possible that *Zoosphaerium stigmaticum* may represent an Australian Sphaerotheriida, the only group of giant pill-millipedes in which such a sclerotized knob is common. The only known type specimen seems no longer to exist.

Zoosphaerium glabrum (Butler, 1873)

Sphaerotherium glabrum Butler, 1873: 173, pl. 19, figs 1-1a. — de Saussure & Zehntner 1897: pl. 4, fig. 3 (reprint of Butler's figure); 1902: 34 (lists species name).

Zoosphaerium glabrum – Jeekel 1999: 9 (lists species name). — Enghoff 2003: 620 (lists species name).

REMARKS

The first description is not suitable for species identification, the only known type specimens seems no longer to exist.

Zoosphaerium latum (Butler, 1872)

Sphaerotherium latum Butler, 1872: 358, pl. 18, fig. 3. — Butler 1873 (lists species name). — de Saussure & Zehntner 1897: pl. 5, fig. 14; 1902: 49.

Zoosphaerium latum – Jeekel 1999: 11 (lists species name). — Enghoff 2003: 620 (lists species name).

REMARKS

The specimens used for redescription by de Saussure & Zehntner (1902) are no longer in the collections of the MNHN, but the published drawings identify it as identical with *Zoosphaerium neptunus*. The first description is not suitable for species identification and the type specimens are presumably lost.

Zoosphaerium lamprinum (Butler, 1878)

Sphaerotherium lamprinum Butler, 1878: 300. — de Saussure & Zehntner 1897: pl. 5, figs 17-17b; 1902: 38.

Zoosphaerium lamprinum – Jeekel 1999: 11 (lists species name). — Enghoff 2003: 620 (lists species name).

REMARKS

All specimens used for redescription by de Saussure & Zehntner (1902) were studied (MNHN CB033). All are young immatures, furthermore their body is abnormally shaped (fixed in formalin?). It is unclear if de Saussure & Zehntner studied the holotype, which was stored at the BMNH, but cannot be traced in the collection. The provided drawing clearly shows a female of *Zoosphaerium neptunus*.

Zoosphaerium? testaceum (Olivier, 1792)

Julus testaceus Olivier, 1792: 414.

Zephronia testaceus – Gervais 1837: 43 (lists species name); 1847: 86 (lists species name). — Butler 1873: 179 (lists species name).

Sphaerotherium testaceus – Brandt 1841: 364 (lists species name). — de Saussure & Zehntner 1902: 69 (lists species name).

Zoosphaerium testaceum – Jeekel 1999: 15 (lists species name). — Enghoff 2003: 620 (lists species name).

REMARKS

The first description is not suitable for species identification and the type specimens are presumably lost.

DISCUSSION

Since this work is the first revision ever undertaken in Malagasy giant pill-millipedes, the discovery of seven synonymies among 27 studied species (Table 1) is not such a surprise. Most of the synonymized names are those of species described by de Saussure & Zehntner (1897, 1902) (Table 1). These mistakes could have happened because the authors had only few specimens

TABLE 1. — Valid species of Malagasy Sphaerotheriida Brandt, 1833.

Species	Synonymies newly proposed in this paper	Remarks	Ecosystem
<i>Sphaeromimus musicus</i> (de Saussure & Zehntner, 1897)	—	—	dry forest, gallery forest
<i>S. splendidus</i> Wesener & Sierwald, 2005	—	—	littoral rainforest
<i>S. inexpectatus</i> Wesener & Sierwald, 2005	—	—	littoral rainforest
<i>Microsphaerotherium ivohibiense</i> Wesener & Van den Spiegel, 2007			montane rainforest
<i>Zoosphaerium neptunus</i> (Butler, 1872)	<i>Z. digitale</i> (de Saussure & Zehntner, 1897) <i>Z. pygidale</i> (de Saussure & Zehntner, 1897)	—	rainforest
<i>Z. campanulatum</i> (de Saussure & Zehntner, 1897)	—	—	rainforest
<i>Z. libidinosum</i> (de Saussure & Zehntner, 1897)	—	—	spiny forest
<i>Z. arborealis</i> Wesener & Sierwald, 2005	—	—	rainforest, littoral rainforest
<i>Z. lambertoni</i> (Brolemann, 1922)	—	—	?
<i>Z. priapus</i> (de Saussure & Zehntner, 1897)	—	—	littoral rainforest
<i>Z. anomalum</i> (de Saussure & Zehntner, 1902)	—	—	montane rainforest
<i>Z. alluaudi</i> (de Saussure & Zehntner, 1897)	—	—	littoral rainforest
<i>Z. voeltzkowianum</i> (de Saussure & Zehntner, 1897)	<i>Z. imbecillum</i> (de Saussure & Zehntner, 1897) <i>Z. globulus</i> (de Saussure & Zehntner, 1902)	—	rainforest
<i>Z. coquerelianum</i> (de Saussure & Zehntner, 1897)	<i>Z. amittum</i> Chamberlin, 1921 <i>Heligmasoma errans</i> Chamberlin, 1921	—	?
<i>Z. villosum</i> Wesener & Sierwald, 2005	—	—	littoral rainforest
<i>Z. platylabum</i> (de Saussure & Zehntner, 1897)	—	—	rainforest
<i>Z. subreflexum</i> Jeekel, 1999	—	—	montane rainforest
<i>Z. blandum</i> (de Saussure & Zehntner, 1897)	<i>Z. stridulator</i> (de Saussure & Zehntner, 1897)	—	dry forest
<i>Z. piligerum</i> (de Saussure & Zehntner, 1897)	—	—	montane rainforest
<i>Z. sakanum</i> (Attems, 1910)	—	—	rainforest
<i>Z. fraternarium</i> Jeekel, 1999	—	—	?
<i>Z. immane</i> (Karsch, 1881)	—	—	?
<i>Z. anale</i> (de Saussure & Zehntner, 1897)	—	—	?
<i>Z. ? reticulatum</i> (Butler, 1878)	—	—	?
<i>Z. actaeon</i> (White, 1859)	—	<i>nom. dub.</i>	?
<i>Z. hippocastanum</i> (Gervais, 1847)	—	<i>nom. dub.</i>	?
<i>Z. reflexum</i> (Brolemann, 1922)	—	<i>nom. dub.</i>	?
<i>Z. elegans</i> (Lenz, 1880)	—	<i>nom. dub.</i>	?
<i>Z. crassum</i> (Butler, 1878)	—	<i>nom. dub.</i>	?
<i>Z. stigmaticum</i> (Butler, 1873)	—	<i>nom. dub.</i>	?
<i>Z. glabrum</i> (Butler, 1873)	—	<i>nom. dub.</i>	?
<i>Z. latum</i> (Butler, 1872)	—	<i>nom. dub.</i>	?
<i>Z. lamprinum</i> (Butler, 1878)	—	<i>nom. dub.</i>	?
<i>Z. ? testaceum</i> (Olivier, 1792)	—	<i>nom. dub.</i>	?

of each species, often only one individual in one sex. The fact that almost all previous researchers avoided the laborious comparisons with the often insufficiently described type material further attributed to the large list of synonym names.

More surprisingly is the fact, that from the 70 morphospecies of the genus *Zoosphaerium* discovered in recent collected material (Wesener 2006) only eight could be assigned to an existing species name. Those findings highlight the fact, that the

giant pill-millipede fauna is insufficiently known, most species still undescribed. Because of the ongoing destruction of natural forest on Madagascar (Green & Sussman 1990; Dufils 2003) and the small area of distribution of many Malagasy millipede species, the inventory work of those neglected groups of soil invertebrates should rapidly speed up in order to at least describe and preserve endemic species before they will become extinct.

This study is only a first step towards a comprehensive study of Malagasy Sphaerotheriida. Numerous species are awaiting their description (Wesener 2006).

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